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Anthropological Perspectives on Tooth Morphology

Genetics, Evolution, Variation

Edited by
G. Richard Scott and Joel D. Irish

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Cambridge Studies in Biological and Evolutionary Anthropology 66

Anthropological Perspectives on Tooth Morphology

Researchers have long had an interest in dental morphology as a genetic proxy to reconstruct population history. Much interest was fostered by the use of standard plaques and associated descriptions that constitute the Arizona State University Dental Anthropology System, developed by Christy G. Turner II and students. This system has served as the foundation for hundreds of anthropological studies for more than 30 years.

In recognition of this success, this volume brings together some of the world's leading dental morphologists to expand upon the concepts and methods presented in the popular *The Anthropology of Modern Human Teeth* (Cambridge 1997), leading the reader from method to applied research. After a preparatory section on the current knowledge of heritability and gene expression, a series of case studies demonstrate the utility of dental morphological study in both fossil and more recent populations (and individuals), from local to global scales.

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Acknowledgments

It is not specifically stated in the title, but a key purpose of this volume is to honor Professor Christy G. Turner II. Without him and his research, it is doubtful that the study of dental nonmetric traits would be as important to the field of biological anthropology as it is today; indeed, many chapters herein could not have been written, or would necessarily be quite different in approach, content, and result. One reason, of course, relates to Turner's conception of and contribution to the creation of the Arizona State University Dental Anthropology System (ASUDAS). An extension of the Dahlberg dental plaques, it is considered by researchers around the world to be the "gold standard" for standardized recording of dental morphological features. Further, Turner's application of the ASUDAS sheds new light on the peopling of the Americas, including his idea of three migrations from Northeast Asia (which recently received support from genetic research); he also introduced a research framework emulated by several of the present authors, including the volume editors. On that note, we (GRS and JDI) cannot speak for the others, but we can unreservedly state that Turner significantly influenced our careers and helped make us what we are today (for better or worse!). Additional background on the life and times of Christy G. Turner II is presented within the volume.

An edited volume can only be assembled through the cooperation and good graces of its many contributors. We thank the authors who participated in the AAPA symposium and then provided chapters on their presentations. Several other authors generously filled in blanks for topics not covered in the symposium (including the editors). Our editor at Cambridge University Press, Lynette Talbot, and other Cambridge University Press staff, including Martin Griffiths and Zewdi Tsegai, helped put all the pieces together. We also thank Cambridge University Press in general for their commitment to biological anthropology, reflected in their production of a wide-ranging set of books that cover the gamut of the field from genes and primates to fossil hominids and teeth.

Individually, GRS thanks Christy G. Turner II for pointing him toward teeth in 1968, which, at the time, was no easy task. He also thanks his wife, Cheryl, and boys, Garrett, Geoffrey, and Gunnar, for their constant inspiration.

JDI thanks Christy G. Turner II for providing incisive dental anthropological advice and suggesting that Africa be the geographic focus of such study. Lloyd and Violet Irish provided lifelong support, and Carol Irish has been working on it for the past 18 years and counting.

1 *Introduction*

G. RICHARD SCOTT AND JOEL D. IRISH

1.1 Christy G. Turner II and 50 years of dental anthropology

Although "festschrift" is not in the title of this volume, it should be. A festschrift is "a book honoring a respected person, especially an academic, and presented during his or her lifetime" (Wikipedia). In all respects, this work mirrors that definition. This volume emanates from a symposium organized by the editors in honor of Regents' Professor Christy G. Turner II (Figure 1.1), held in 2010, Albuquerque, New Mexico, at the 79th annual meeting of the American Association of Physical Anthropologists.

Motivated by the research of Bertram S. Kraus (University of Arizona) and Albert A. Dahlberg (University of Chicago) during his graduate student days (see Chapter 2), Turner decided teeth were the perfect tool to address issues of population origins and relationships. From Kraus, he was inspired to explore the genetic underpinnings of tooth crown morphology. From Dahlberg, he was inspired to utilize and improve observational standards so the field of dental morphology could move beyond its old bugaboo, interobserver error (Turner 1967a; Turner et al. 1991).

From 1970 to 1990, Turner worked on new ranked standards for crown and root trait classifications and scored morphological traits in ca. 30,000 skulls in scores of museums throughout the Americas, Asia, the Pacific, and Europe (in that order). Using the Dahlberg plaques as a foundation, Turner (see this volume) and his students developed many classificatory standards during the 1970s and 1980s, ultimately culminating in the Arizona State University Dental Anthropology System (ASUDAS; Turner et al. 1991). His ultimate goal was not simply to develop standards of observation; instead, it was to use these standards to address anthropological problems on local, regional, and global scales.

Anthropological Perspectives on Tooth Morphology: Genetics, Evolution, Variation, eds. G. Richard Scott and Joel D. Irish. Published by Cambridge University Press. © Cambridge University Press 2013.

Figure 1.1. Regents' Professor Christy G. Turner II.

From the simple foundation of an accessory root on the lower first molar (three-rooted lower first molars, or 3RM1; see book cover and Turner 1971), Turner developed a three-wave model for the peopling of the Americas that led to a collaboration with Joseph Greenberg and Steven Zegura in a paper entitled "The settlement of the Americas: a comparison of the linguistic, dental, and genetic evidence" (Greenberg et al. 1986). For the next 20 years, every researcher who published on colonization of the New World was compelled to discuss it in light of the three-wave model (whether in agreement or not). In the process of scoring thousands of Native American and Asian dentitions, Turner (1990) also found a dichotomy between North Asians (Sinodonts) – the source populations for the Americas – and Southeast Asians (Sundadonts) – the source populations for the Pacific. To the initial chagrin of Japanese physical anthropologists, he used dental morphology to show the prehistoric Jomon peoples were linked to Ainu and not the modern population of Japan; the latter instead came from the Asian mainland about 2,200 years ago (Turner 1976).

Given the enormous number of frequent flier miles he was accumulating, Turner's colleagues and students thought he was trying to look at every dentition on the planet. But alas, there were far too many, even surpassing his zeal for travel and collections research. To extend the realm of dental morphology, he encouraged Joel Irish (1993) to take on the colossal task of African

dental variation, Sue Haeussler (1996) to observe early and late Siberians and Central Asians and tie them to New World groups, Diane Hawkey (1998) to study early and late samples on the Indian subcontinent, Alma Adler (2005) to observe Scots in the context of northern European dental variability, and Christine Lee (2007) to do in-depth research in China and Mongolia. And those were only his PhD students. Master's degree students were also sent far and wide to pursue regional studies of dental morphology, including Mary Larsen (1978), Lorrie Lincoln-Babb (1999), and Stephen Reichardt (2000) in Native American groups; Kathy Roler (1992) and Jaime Ullinger (2002) in the Middle East; Joshua Lipschultz (1996) in northeast Africa; and Jaimin Weets (1996) in Melanesia. This list only takes into account those students whom Turner supervised as graduate students. His work stimulated many more students to write MA theses and PhD dissertations on dental morphology in not only the United States but Europe and Asia as well.

This volume is in many respects a sequel to *The Anthropology of Modern Human Teeth: Dental Morphology and Its Variation in Recent Human Populations* (AMHT; Scott and Turner 1997). In other regards, it is an expansion. In AMHT, there was a chapter on genetics, but this predated the many developments involving homeotic genes, epigenotypes, and evo-devo in general. There was reference to fossil hominin dental morphology in the epilogue, but that topic fell beyond the expertise of the authors, who never systematically studied fossil dentitions. Some comments were directed at the use of dental morphology in assessing ethnicity in forensic studies and morphological studies of deciduous teeth, but these topics were not developed at the time. The main focus of AMHT was variation in the permanent dentition of recent human populations. In the 15 years since its publication, morphological variation has been pursued to every corner of the earth. The aim of the present work is to turn major topics over to subject area experts who can provide the problems, context, and references for the major divisions of this book on human tooth morphology: genetics and evolution, fossil hominins, and variation in recent human populations. The symposium in Albuquerque was limited to fourteen contributors; the present volume includes twenty chapters to broaden further the topics that fall within the realm of human dental morphology.

1.2 Genetics and evolution

For tooth morphology to have any currency in assessing population affinities, individual traits should have a strong heritable basis. Early twin studies suggested that dental morphology and agenesis were hereditary (Bachrach and Young 1927; Montagu 1933; Newman 1940), but the modes of inheritance

of specific traits remained unknown. One early attempt to ascertain mode of inheritance through a pedigree study focused on Carabelli's trait. On the basis of one large and seven small pedigrees, Kraus (1951:354) concluded that the trait segregated in a manner consistent with "2 allelic autosomal genes without dominance" (i.e., intermediate dominance or codominance). While writing his dissertation, Turner used the Hardy-Weinberg formula and goodness of fit tests to determine whether class frequency distributions were consistent with codominant inheritance. For the most part, traits did conform to expectations; as such, he took the next step and calculated gene frequencies for shoveling, Carabelli's trait, the hypocone, and protostylid. He published two papers in which he calculated "gene frequencies" for dental morphological traits to help measure gene flow (Turner 1967b, 1969). Despite this innovative approach, anthropological geneticists were critical of using population data to determine modes of inheritance, forcing him to change directions.

Knowing how important it was to understand the genetic basis of morphological traits, Turner encouraged students to test modes of inheritance using family data. Three dissertations directed at this issue ultimately concluded that crown traits were quasi-continuous variables with polygenic modes of inheritance (Scott 1973; Harris 1977), with major gene effects suggested for some (Nichol 1990). Although morphological traits could not be reduced to gene frequencies, there was now a rationale for using total trait frequencies for population characterizations and comparisons (cf. Falconer 1960).

Since 1990, the revolution in human genomic analysis and an enhanced appreciation of homeotic genes have greatly altered our perspective on the genetics of tooth morphology. This is evident throughout the five chapters in the section on genetics and evolution. According to the experimental work of Jukka Jernvall and his collaborators, there is no simple one-to-one relationship between a particular dental trait and gene. However, the general attribution of polygenic inheritance is becoming more refined; development is not regulated by many genes – each acting with small effects – but rather a finite number of genes operating in concert. They operate in developmental modules to produce a final form, or phenotype.

Although experimental work on rodents has been generalized to mammalian dental development (Jernvall and Jung 2000), genetic research on humans is still required to address questions relative to human crown morphology. Hughes and Townsend review advances in odontogenesis, including the identification of specific genes involved in dental development. Their primary emphasis is on the contribution of twin analyses to genetic studies of tooth size, shape, and morphology. With extensive biological information on >1,200 Australian twin pairs, they summarize heritabilities for crown size, intercuspal distance, agenesis, supernumerary teeth, and crown morphology, including Carabelli's trait;

cusps 5, 6, and 7; and the hypocone. The heritability calculated for Carabelli's trait is around 90 percent, a value notably higher than that found in smaller twin studies and one that suggests a strong genetic component for this classic trait. Traditionally, twin studies stopped at heritability estimates, but Hughes and Townsend note how analysis can go beyond h^2 ultimately to identify the genes involved in development.

Guatelli-Steinberg and colleagues demonstrate how developmental genetics can guide research questions in dental morphological studies. Following principles of the "morphodynamic model" (Salazar-Ciudad and Jernvall 2002, 2010), they evaluate the presence and size of Carabelli's trait relative to intercusp spacing, tooth size, and the hypocone; they also consider trait variability between males and females, antimeres, and metameres. Earlier studies noted relationships between Carabelli's trait expression and tooth size, the hypocone, and protostylid; an understanding of how primary and secondary enamel knots and their activator and inhibitor molecules moderate development of major and minor cusps has greatly advanced our knowledge of crown trait formation, along with the interplay of size and morphology.

Rizk and colleagues present a detailed review of dental ontogeny that includes a discussion of specific genes and gene products in the developmental cascade leading to tooth formation. The primary aim of their chapter, however, is to discuss the advantages of the rapidly advancing field of geometric morphometrics (GM). Applications are reviewed for a wide variety of mammals, especially rodents; however, their specific focus is on the dentition of the Old World monkey *Colobus guerza*. The authors approach phenotype from a different perspective than traditional studies, using GM to focus on the entire tooth row and specific elements within the row rather than conventional measurements. When this approach is applied to mammalian dentitions, including our own, it should greatly enhance our understanding of long- and short-term dental evolution.

As a pioneer in studying the effects of chromosomal nondisjunction on dental development, Alvesalo compares cephalograms and dental casts across a wide range of chromosomal syndromes (e.g., XO, XXY, XYY, etc.) to determine how variations in the number of X and Y chromosomes contribute to crown size, structure, and shape, along with root form and craniofacial patterns. Shovel-shaped incisors, for example, differ between individuals with certain syndromes and both their relatives and the general population. This approach complements the use of twins and families in showing how genes on the X and Y chromosomes contribute to tooth size, shape, morphology, and craniofacial dimensions.

Mizoguchi addresses an issue that has long befuddled dental morphologists. Are the accessory ridges, fossae, cusps, and fused or accessory roots that make

up the panoply of dental morphological traits subject to natural selection or is their variation a product of chance? Harkening back to the selectionist versus neutralist debates, many of us (cf. Scott and Turner 1997; T. Hanihara, this volume) feel that most variation among recent human populations is attributable to genetic drift and founder effect. Others, including Mizoguchi, feel these variables are either directly or indirectly affected by selection. While it would be difficult to demonstrate that Carabelli's cusp contributes to survival or reproduction, Mizoguchi argues this feature (and others) is tied developmentally to biochemical, climatic, and/or cultural variables that are more demonstrably impacted by selection. The key to this approach is finding how dental traits fit within larger biological complexes that are subject to overt selective pressures.

1.3 Fossil hominins

The crown and root morphology of recent human populations can only be fully appreciated in light of earlier hominin ancestors. There are classic works on fossil teeth, such as Franz Weidenreich (1937) on *Sinanthropus pekinensis* and J.T. Robinson (1956) on South African australopithecines, but most early workers described every crest, ridge, and tubercle on each tooth without putting those characteristics into a population context (e.g., normal, rare, common). Wood and his colleagues were among the first to tabulate frequencies for crown and root traits in australopithecines and early *Homo,* providing an invaluable perspective on primitive and derived conditions (Wood and Abbott 1983; Wood and Engleman 1988; Wood and Uytterschaut 1989; Wood et al. 1983).

Taking on the thorny issues of hominid origins and Plio-Pleistocene dental variation, Schroer and Wood describe crown and root traits and form in not only early hominins (*Australopithecus* and *Homo*) but also early fossils that may or may not be hominin (e.g., *Sahelanthropus*, *Orrorin*, *Ardipithecus*, *Kenyanthropus*). In delineating "primitive" and derived traits, they come up with a suite of characteristics that defines the "most recent common ancestor" (MRCA) of modern humans and chimpanzees/bonobos. Their conclusions regarding the hominid/hominin status of various fossils may surprise early "fossil hunters" who have a vested interest in the taxonomic status of their discoveries. For future fossil finds, Schroer and Wood make predictions on what characteristics of postcanine macromorphology should be present in the MRCA of hominines and panins/hominins, as well as in the stem taxa of the gorilla, chimpanzee/bonobo, and human clades.

Over the past 20 years, a confluence of events has resulted in an increased level of interchange between researchers who work primarily with fossil

hominin dentitions and those who work with recent human populations. For one, the standards outlined by Turner et al. (1991) have been utilized to make observations on Neanderthals (Bailey 2002), Middle Pleistocene hominids from Atapuerca and Sima de los Huesos (Bermúdez de Castro 1988, 1993; Martinón-Torres et al. 2012), and early Pleistocene hominids from Dmanisi (Martinón-Torres et al. 2008). These researchers have discovered, perhaps not surprisingly, that the ASUDAS standards are not always directly applicable to earlier hominins. For the most part, earlier and recent humans express the same traits. The issue is that Neanderthals and *Homo heidelbergensis* dental characters often fall outside the range of the ASUDAS standards, which were based on recent *Homo sapiens* crown and root morphology.

Martinón-Torres and her colleagues describe the large sample of Middle Pleistocene hominin teeth from the site of Sima de los Huesos (SH) in northern Spain. In many respects, the 400,000- to 500,000-year-old teeth from this site show close parallels to later Neanderthals. For example, the classic anterior tooth combination of pronounced shoveling, labial convexity, and *tuberculum dentale* typifies both groups. However, in SH, there is more dental reduction than in Neanderthals, and this involves both tooth size and the loss of cusps. How SH shares some characters with Neanderthals and others with modern humans is an intriguing finding that should stimulate new lines of analysis.

Bailey and Hublin complement the article by Martinón-Torres and her colleagues by addressing the issue of what nonmetric dental traits set *Homo sapiens* apart from earlier species of Homo (e.g., *Homo heidelbergensis, H. erectus*). Their observations show how far the field has advanced in the past 60 years. Franz Weidenreich (1937) thought incisor shoveling linked *Sinanthropus* (lower cave Zhoukoudien) to modern Chinese. As Bailey and Hublin note, shoveling was ubiquitous in earlier hominids, including Neanderthals and *H. heidelbergensis.* It remains highly variable among modern humans, including pronounced reductions in frequency and expression in Western Eurasians and Africans. One trait that seemingly sets modern humans apart is hypoconulid loss on the lower first and second molars. Four-cusped first and second molars are in a ratio of about 10:80 in most Western Eurasian populations, but the distinctness of these frequencies is offset by relatively high frequencies in the sample from Sima de los Huesos. Tooth size reduction, also seen in modern humans and the SH sample, may be implicated in this similarity. The one trait that sets Neanderthals and SH apart from modern humans is the middle trigonid crest. This trait was not even discussed in *The Anthropology of Modern Human Teeth* because it is so rare in modern humans. In Neanderthals and SH, it is almost always expressed. This distinction is evident not only on the crown surface but also on the dentine-enamel surface. This is the kind of trait that pushes the limits of ASUDAS when applied to the fossil record. Another such

trait is labial convexity. This is typical and pronounced in Neanderthals and SH incisors but is much less common in modern humans. Even when present in modern samples, it never approaches the level expressed in Neanderthals. The appearance of UI1 double shoveling, which occurs only recently in *Homo sapiens*, could be associated with the reduction of labial convexity.

The final contribution on fossil hominins by Macchiarelli and his collaborators is methodological, with examples to illustrate the potential of microfocal X-ray computed tomography. Until recently, researchers were "confined" to external crown and root surfaces. With new technology, we can now view not only the outside but also the inside of a tooth. When this method is more widely adopted, it will revolutionize the field of "virtual dental (paleo)anthropology." The authors use three test cases to show the advantages of this high tech approach to studying teeth. First, they compare antimeres in a well preserved Neanderthal jaw and come up with highly precise measurements of enamel cap volume, dentine volume, pulp chamber volume, and so on. To demonstrate fluctuating asymmetry using conventional calipers and linear measurements is difficult because of the slight differences between antimeres (also compounded by measurement error). Tomographic methods provide far more precise and replicable measurements. Tomography is also used to compare the components of deciduous and permanent teeth in fossil hominins and recent humans and tackle the complexities of root form. The detailed 3-D renderings that can be produced with this method should lead to new research questions on root form and diet. When microtomography becomes readily available in labs throughout the world, it will produce a whole new world of "virtual teeth" and a new set of questions to match.

1.4 Human variation

When we assembled a group of morphologically inclined scholars to provide papers on recent human dental variation, the goal was to cover as much of the world as possible. To a large extent, this was achieved. Major geographic regions of the world covered include Africa (Chapter 12, Irish), Europe (Chapter 13, Scott et al.), Micronesia (Chapter 14, Nelson), South Asia (Chapter 15, Hemphill), China and Mongolia (Chapter 16, Lee and Zhang), and the New World (Chapter 17, Stojanowski et al.). Lukacs and Kuswandari (Chapter 18) focus on a sample from Southeast Asia using deciduous dental morphology, while T. Hanihara (Chapter 19) uses dental morphology and metrics to address the weighty topic of the origins and dispersal of anatomically modern humans.

The papers in this section are a twofold testimony to the legacy of Christy Turner's research on dental morphology. First, the researchers use all or part

of the ASUDAS to collect data on extinct and extant populations (except for deciduous teeth where K. Hanihara's standards are still used). Second, they address both large scale and regional questions of population origins and relationships, an approach Turner advocated throughout his career. Irish takes on the issue of sub-Saharan African variation and coins a new term that encapsulates this variation – "Afridont." While there is variation in sub-Saharan Africa, the so-called Bantu expansion from West Africa had a major impact on recent dental variation. Scott and his collaborators describe the dental morphology of Basques in northern Spain who have long been noted for their unique language and distinct genetic markers. While Basques may be a descendant population from the western European Upper Paleolithic as many have proposed, they fail to exhibit any crown or root traits that would set them clearly apart from Indo-Europeans in particular or Western Eurasians in general. South Asians from India, Pakistan, and Afghanistan show linguistic and genetic ties to populations in the Middle East, but this is a Holocene phenomenon. Hemphill shows how dental variables can be used to infer the timing and movement of populations into South Asia. Exploiting one of the dentition's many advantageous characteristics, he analyzes tooth size and morphology in both extinct and extant populations. He finds there is no serious bias in combining dental data from the living and dead and notes that by using tooth size apportionment methods, the analysis of size and morphology provides similar results in delineating population affinity.

Turning to East Asia, Lee and Zhang note how earlier research combined populations across China and Mongolia into a composite sample as if there was little or no dental variation in the region. Although populations are mostly Sinodont, there is still regional variation. This is especially notable in northwest China, where there was an early Indo-European presence in the Tarim Basin. Although dealing with a small sample, Nelson demonstrates that for Micronesians from Palau, it is still possible to recognize their Sundadont origins. The sample has exceptionally large teeth, and they are morphologically aligned with Southeast Asia. Deciduous teeth receive much less attention than permanent teeth in studies of dental morphology, in part the result of the limitations of small sample size in the archaeological record. Lukacs and Kuswandari analyze the crown morphology of deciduous teeth in a Malay sample to determine whether they conformed to a Sundadont pattern. They found Malay teeth were most similar to those of South Asians in some analyses but were more African in others. The limited comparative samples for deciduous teeth make such evaluations difficult, but with increased attention, workers will start taking advantage of the largely untapped potential of deciduous crown morphology.

In their review of New World dental variation, Stojanowski and his colleagues acknowledge the significant contribution that Turner made in using

dental data to develop models for the peopling of the Americas. However, they challenge the notion that all Native Americans are Sinodonts, as a number of researchers, especially in South America, have observed Sundadont characteristics. Turner has opined that crown wear can make a Sinodont dentition appear Sundadont. Although wear impacts the ability to make morphological observations, as noted by Burnett, Irish, and Fong in Chapter 21, it does not impact roots and even root traits purportedly are in line with Sundadonty rather than Sinodonty. Given the diversity of form in Paleoindian and Archaic crania, it is not surprising there is intercontinental dental variation during these early periods. The authors aver it is time to move beyond Sinodonty and Sundadonty and perhaps this will happen. New methods of analysis and the addition of more traits to augment the ASUDAS should make the issue of New World dental variation more interesting and challenging.

Expanding beyond a single continent, T. Hanihara takes a global view of dental variation and puts it to use in helping resolve the problem of the origins and routes of dispersal of anatomically modern humans. In line with the Irish chapter on Africa, this is the continent that served as the springboard for the peopling of the world. But which route did they take, when did they disperse, and how do these factors impact modern human variation? These are the kinds of broad issues Hanihara addresses. Another question revolves around locating the source population for East/North Asians, or in Turner's parlance, Sinodonts. Turner proposed that Sinodonty originated from a Sundadont base so the likely source of origin would be Southeast Asia. Hanihara, however, finds hints that Central Asia and Siberia may provide additional points of origin for North Asians.

1.5 Methods and prospects

Many of us who "know teeth" and get involved in forensic anthropology utilize crown and root morphology to assess ethnicity. This is usually done in conjunction with craniometric and anthroposcopic traits for the sake of thoroughness. For the skeletal biologists who do not specialize in teeth, tooth morphology is at a decided disadvantage compared to craniometrics for two basic reasons: (1) it is easy to train students to take classic craniometric measurements; and (2) it is even easier to plug these numbers into a discriminant function program (e.g., FORDISC) and get some idea of geographic affinity (whether correct or not).

Edgar and Ousley try to level the playing field for using dental morphology in forensic cases, but this is a work in progress. Using a variety of complex statistics, they arrive at relatively high levels of accurate classification when trying to sort out the basic components of the U.S. population (Euro Americans,

African Americans, Asian Americans, Native Americans, and Hispanics from the Southwest and Florida). There are issues, however, and some groups can be classified more accurately than others. Perhaps Ousley, who helped develop FORDISC, will put his considerable statistical skills to use and arrive at a formula that would allow individuals trained in dental morphology to make probabilistic assessments of ethnicity. Until that happens, tooth morphology will continue to get short shrift in forensic anthropology textbooks (cf. Byers 2011).

The final chapter, by Burnett and his colleagues, is a cautionary tale that all dental morphologists should heed. For those of us who have scored thousands of teeth, we know that crown wear is a serious impediment to making accurate morphological observations. It is likely that we all set our own personal standards for how much wear can be tolerated until we conclude a trait is unobservable. When dealing with large samples (e.g., >100), worn teeth are easily passed over because doing so has little impact on sample size. For small samples, the temptation is greater to make every observation that is even remotely possible. One should always remember, however, that an inaccurate observation is more detrimental to sample frequencies than no observation. When in doubt, leave it out!

1.6 From foundation to action

During the first half of the twentieth century, a number of researchers helped lay the foundation for the study of human tooth morphology, including J.C.M. Shaw, T.D. Campbell, A. Hrdlička, M.R. Drennan, P.O. Pedersen, B.S. Kraus, G.W. Lasker, C.F.A. Moorrees, S.M. Garn, K. Hanihara, D.H. Morris, T. Brown, A.A. Zubov, and A.A. Dahlberg, among others. In 1963, Don Brothwell edited the historic tome *Dental Anthropology*. Of the fifteen papers in that work, four dealt with some aspect of dental morphology. Kazuro Hanihara contributed a paper on the deciduous teeth of Japanese-American hybrids. Virginia Carbonell studied shovel-shaped incisors in a few hundred skulls and casts in ten samples (five European, one African, one Middle Eastern, one Asiatic Indian, one Japanese/Chinese/Tibetan, and one Eskimo). Verner Alexandersen brought together data from nine samples to illustrate a rare but notably European dental variant, two-rooted lower canines. Al Dahlberg provided a classic paper on the American Indian dentition in which he focused on the contrasts between Pima Indian and American White dental morphology.

How times have changed. At the fiftieth anniversary of the publication of *Dental Anthropology*, we would surmise that the contributors who wrote papers on dental morphology for that volume would be stunned by advances in the field. One cannot simply attribute these advances to the passing of time as the

passing of time does not bring advances in all areas of the field. In the 1940s and 1950s, there were many articles written on split-line studies of primate crania. In the 1950s, somatotyping was popular but makes few appearances in the *American Journal of Physical Anthropology* these days. In the 1960s, the *AJPA* published more than forty papers on the skin of primates. Today, the subject is rarely broached.

For a field to develop, you need pioneers who see the potential of a particular avenue of research and you need someone to take that potential and put it into action. Dahlberg, Pedersen, Moorrees, and others saw the potential of tooth morphology, but they had neither the time nor mind-set to develop its anthropological potential. Dahlberg supervised numerous PhD students in the Department of Anthropology at the University of Chicago. While many went on to enjoy great success in the field (e.g., Don Johanson, Philip Walker), none took the next step and built upon the foundation laid by their mentor. That is where Christy Turner came in. He was willing (1) to ask big questions (migrations to the New World and Pacific, modern human origins, etc.); (2) to expend time and energy developing methods (ASUDAS); and (3) to spend hundreds of hours in museums observing thousands of dentitions, putting those methods to the test (too numerous to mention). To advance dental morphological studies in the broader framework of physical anthropology, he had another advantage – graduate students (including the coeditors), and many of them.

From 1968 to 2007, dental anthropology at Arizona State University was a beehive of activity. MA and PhD students worked on issues of oral biology (e.g., genetics, intertrait association), classification (e.g., developing and testing new trait standards), and variation (e.g., analysis of crown and root trait variation throughout the world), along with other avenues of research in dental anthropology (e.g., pathology, linear enamel hypoplasia, cultural modification). "Natural selection" has reduced the significance of many lines of anthropological inquiry over the past 50 years, but it has favored the development of dental morphological studies. Many have contributed to building the current edifice that symbolizes modern studies of tooth morphology, but the current status it enjoys ultimately revolves around the efforts and vision of Regents' Professor Christy G. Turner II, to whom this volume is dedicated.

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2 *Bite marks in tule quids: the life and times of a dental anthropologist*

CHRISTY G. TURNER II

2.1 Introduction

Teeth wear out, hearts fail, and memories fade. But it is impossible for me to forget the young and older scholars identified on pages 25–26. In addition to their original contributions to dental anthropology, they have provided moments of unforgettable courage. For example, who could forget the morning of Mahmoud El-Najjar's oral dissertation defense. Earlier that morning the screaming headline of the largest Arizona newspaper said: "Number 2 PLO killed." This person was Mahmoud's Palestinian brother. When we asked Mahmoud whether he would like to reschedule the examination, given the shocking news, he quietly said no. The oral defense proceeded and Mahmoud performed excellently. And who could forget another oral examination where a young woman tried to answer questions with tears streaming down her cheeks and her voice strangled in her terror of the event. I believe that my extended earthly existence has been aided by the intellectual stimulation that these wonderful people have given me. I keep in touch with some, but others have disappeared, some from death, some from personal problems, some from changes in their interests, and some from simply not keeping in touch.

With humility and much pride in these Arizona State University students who have done research in dental anthropology, I relate herein what I can recall about my career in the field. I do so at the request of G. Richard Scott and Joel D. Irish. Dental anthropology has been the major aspect of my professional life, although I continue to have other interests. This is not the place to discuss them, but they involve topics as diverse as prehistoric cannibalism, rock art, and perimortem taphonomy. Fundamentally I am an empiricist and an evolutionist. These perspectives have colored all my thinking and still do.

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2.2 Highlights of my dental anthropology career

My interests and activities in human dental research can be divided into five chronological stages linked with my institutional affiliations: (1) University of Arizona, Tucson (1955–1958); (2) Museum of Northern Arizona, Flagstaff (1956–1961, and later years); (3) University of Wisconsin, Madison (1961–1963, 1966); (4) University of California, Berkeley (1963–1966); and (5) Arizona State University, Tempe (1966–2004). I was forced to resign from Arizona State University by poor vision caused by macular degeneration. My field research ended in Siberia in 2006, when I made my last observations on late Pleistocene bone fragments and teeth on a gray rainy day. These archaeological finds were curated in a grim run-down multistoried Soviet era office-factory building. That day my field notes included:

> Aug. 12, Sat., Krasnoyarsk…cloudy, cool in a.m.….Breakfast – orange, bread, butter, coffee…Hot water this morning [in old university student dormitory]. N.O. [Nicolai Ovodov, a member of our Siberian taphonomy project] arrived at 10:00 a.m. We walked about 5 blocks to busy bus stop (just past KGB building) … [eventually we reached the place where archaeologist Nicolai Drozdov's collections were stored. Ovodov, my Russian wife, Olga Pavlova, and I] looked at all pieces [from 2006 excavations in late Pleistocene site of Afontova Gora] … perhaps 5,000 total. Could identify no pieces that looked human to me.

During a half century of research, my dental anthropology interests focused on five main topics: (1) production of standardized reference plaques, (2) peopling of the Pacific Basin and adjoining areas, (3) the dental morphology of major modern human populations, (4) dental genetics and microevolution, and (5) environmental effects on teeth. Near the end of my career, I developed a sixth interest: the relationship between European Neanderthals and Cro-Magnons based on dental morphology, an interest that arose from my taphonomic and bioarchaeological research in Siberia. My vision began to fail rapidly in the late 1990s, so I would not give as much attention to this topic as I would have liked. For this reason I urged Shara Bailey to work on the topic, which she did for her PhD dissertation.

2.3 Influences

2.3.1 University of Arizona (UA)

My dental anthropology interests were born in Tucson as a result of the considerable influence of physical anthropologist Bertram S. Kraus. The main influence was his research on dental morphology that indicated a strong genetic

component in crown variation. At the UA Anthropology Department's Point of Pines archaeological field school on the central Arizona Apache Reservation, I encountered my first human burials. These were cremations from an Archaic site called Cienaga Creek. The remains ignited my desire to learn more about dental morphology and make use of teeth for affinity assessment based on Kraus's genetic analyses. Were these Archaic people biological ancestors of the desert Hohokam as their fire-polished mortuary stone projectile points suggested to Emil "Doc" Haury, director of the field school? Kraus's research suggested dental morphology, with its strong genetic component, could possibly be as useful as blood groups for assessing intergroup affinity. At that time, blood group studies could only be done with living individuals, although experiments were being conducted on paleoserology.

Two UA graduate students were also influential: Richard G. Snyder, whose dissertation dealt with teeth of the Pueblo period Point of Pines Indians, and Donald H. Morris, who worked on the dentition of living Papago Indians. Don and I would eventually become close colleagues at Arizona State University, working together for some 40 years.

2.3.2 Museum of Northern Arizona (MNA)

My experiences at this private museum and research center in Flagstaff were wide-ranging and very important to my embryonic career as an anthropologist. The museum in the 1950s and 1960s was a rich bubbling intellectual stew containing the finest ingredients. Jacqueline Adams, whom I would marry in 1957, and I were asked by the new director, Edward B. "Ned" Danson Jr., to serve as summer assistants in 1956 and 1957. He knew us because he was field supervisor at Point of Pines when we three were there in 1955. At MNA, Jackie assisted in geology and I was the summer photographer. Ned wanted me to photograph every possible aspect of the museum's activities, including the major annual summer shows. The museum was staffed by dynamic older and new personnel, whom we assisted in many ways; we also helped many visiting scholars in a wide variety of sciences. MNA was an actual functioning multidisciplinary environment.

Housing for summer assistants and visiting scholars was located on the museum grounds. Housing consisted mostly of converted chicken coups, constructed in the days when the property was an old farm. This communal living made summers in the pines at MNA a heady and fascinating learning experience, interacting with some of world's finest natural and social scientists: T. Dobzhansky, geneticist; Keith Runcorn, plate tectonics; "Major" Brady and John Vance, paleontologists; Charles and Florence Voegelin, linguists; and their many Indiana University

graduate students; David A. Breternitz, the new archaeologist and curator of anthropology; Harold S. Colton, zoologist-archaeologist; and many others.

Unfortunately, scientific research at MNA has fallen on hard times, leaving for the most part only its art exhibit component. I was lucky to have been part of this remarkable museum created by Harold S. Colton and his brilliant artist wife, Mary Russell Colton. Their genius was carried on by the new director, "Ned" Danson. While there were influential "big names" at MNA in the later 1950s, there were influential "little names" also. Three staff members stand out: custodian-carpenter Milton Wetherill, who was past superintendent of Navajo National Monument, and related to the famous pioneering archaeologist Richard Wetherill; Frances Wetherhold, publication editor; and Barton A. Wright, artist, archaeologist, and museum curator. During our years as summer assistants I had access to the collection of human skeletal remains. I would spend many evenings after supper examining prehistoric Anasazi and Sinagua teeth.

From 1958 to 1961 Jacqueline and I were chosen to be part of the MNA Glen Canyon Project, a huge scientific (archaeology, history, geology, biology) salvage program in what would become the area flooded by a miles-long (2,000 miles of shoreline) lake formed by the 710-foot Glen Canyon dam. I wore several hats on the MNA-GCP team. My tasks included archaeology, all photography, much report writing, and physical anthropology. Back at the museum much of my time was devoted to writing reports describing the results and analyses based on our field work. There was little physical anthropology to do because we found few human remains; thus, I was not growing in the anthropological field I wanted to work in. For this reason, I resigned in 1961 to return to school for advanced training in physical anthropology.

The years at MNA were unquestionably the best of my professional and personal life as far as feasting at the table of knowledge. At MNA the menu included a vast array of natural history dishes; marvelous side dishes of Indian culture, prehistory, and art; and an addictive craving to learn about human origins as evidenced by dental morphology. MNA prepared me to take the plunge to the next level, as "Doc" Haury told me: "go somewhere else than here to enhance your physical anthropological interests." I did so, and my choice was the University of Wisconsin, where I learned of an anthropologist whose multidisciplinary interests were almost the same as mine – except he was interested in the Arctic, while I, at the time, was just beginning to deal with the American Southwest.

2.3.3 University of Wisconsin, Madison (UW)

Arctic bioarchaeologist William S. Laughlin accepted me as one of his graduate students and provided me with a two-year research assistantship.

Among my various tasks was a dental study of the Hudson Bay Eskimo skeletal assemblage that Laughlin had on loan from Canada. These observations would be incorporated into my 1967 PhD dissertation, which was eventually published in book form (Turner 1991). Years after his trip to the Aleutian Islands with Smithsonian anthropologist Aleš Hrdlička, Laughlin returned in 1948 to lead a Peabody Museum of Harvard University multidisciplinary expedition. Two expedition participants, who would become highly regarded dental scholars, were Stanley M. Garn and Cambridge dentist Coenraad F.A. Moorrees; the latter's dental study of living Aleuts resulted in the now-classic book *The Aleut Dentition* (Moorrees 1957). In 196l, Laughlin headed another Alaskan expedition. Participants in this trip to Kodiak Island included the anthropologically oriented dentist Albert A. Dahlberg and his wife, Thelma, who together collected Koniag dental impressions and genealogical information as Moorrees had done in the Aleutians. In 1962, with more Alaskan research sponsored by NSF, Laughlin appointed me as summer archaeological field supervisor. At Nikolski village, Umnak Island, I used rainy days, when excavation was impossible, to make dental impressions of Aleuts born after Moorrees's 1948 study. Before I began to make formal observations on Arctic dental morphology, the subject of my dissertation proposal, I spent a week in Dahlberg's Zoller Dental Clinic laboratory at the University of Chicago; there I learned how to use his plaques for standardized observations of tooth crown variation.

In addition to dental casts and prehistoric human skeletal remains we collected in 1962 at Nikolski, the next summer I added crown, root, and other dental observations in northern cranial collections from three eastern U.S. museums. During these visits, I met scholars interested in the anthropological potential of my research. At the National Museum of Natural History (NMNH) in Washington, D.C., there were extensive collections of archaeologically derived Alaskan skeletons excavated by Aleš Hrdlička, Henry B. Collins Jr., and others. At the NMNH, I met J. Lawrence Angel and T. Dale Stewart, osteological experts whom I would meet again and again during my subsequent data collecting trips that focused on non-Arctic populations. That summer, I drove to New York to collect dental data at the American Museum of Natural History. There I met Harry L. Shapiro, who permitted me to study any crania except those in the Alaskan Ipiutak collection, which he said he was going to analyze. He never did.

My last stop of the summer was at the Peabody Museum of Archaeology and Ethnography, Harvard University. I met J.O. Brew and William W. Howell. While neither worked with teeth, both were interested in what I was attempting to accomplish by using dental morphology for intergroup affinity assessments. In Brew's case, he was interested in relationships among southwestern U.S.

Indian groups, while Howell had a long history of studying the population history of Oceanic groups. In later years I would tackle both of their interests.

By the end of summer 1963, I had made morphological, metrical, and environmental observations (wear, caries, chipping, labret facets, etc.) on the teeth of 427 northern individuals that I grouped into nine cultural and linguistic subsamples for analytical purposes. The analyses confirmed the views of Pedersen and Moorrees that (1) Eskimos and Aleuts were ultimately of Asian origin, and (2) both were dentally more closely related to one another than either was to northern Indians. This work pretty much put an end to the theory that Eskimos originated in the forests of Canada. I also countered Moorrees's proposal that the teeth of Western Aleuts evidenced more Russian admixture than those of Eastern Aleuts, mainly due to the frequency of Carabelli's cusp. The archaeological samples of Aleut teeth showed that the east–west frequency difference existed before Russian contact. I proposed that the regional differences arose because of prehistoric microevolution involving a founder effect in small groups migrating westward, with some frequency smoothing caused by later back-and-forth interisland gene flow. This interpretation did not sit well with one of my PhD committee members, who insisted that evolution did not work that way. Despite the disagreement, my 1967 dissertation was selected for publication years later as one of the thirty-three best U.S. dissertations on the evolution of North American Indians (Turner 1991).

2.3.4 University of California, Berkeley (UCB)

In fall 1963, my wife, Jacqueline; daughters Kali Ann and Kimi Lee; and I moved to El Cerrito near the UCB campus where I would teach for the next three years. Our third daughter, Korri Dee, was born in Berkeley. She, unlike the older two, did not experience much of the antiestablishment and countercultural free speech and civil rights movements that rocked early 1960s Bay Area communities. I was on the freeway to San Francisco to attend an American Association of Anthropology session when I heard over the car radio that President Kennedy had been assassinated. Student protests and clashes with police on and off campus involved thousands of people. It quickly became, as is often said, "a perfect storm." Amid the explosive turmoil I was grappling with four personal problems: (1) I had a young and vulnerable family to care for; (2) I was developing new courses for a teaching career that I had no prior experience with; (3) I was trying to finish my doctoral dissertation; and (4) the swirling social chaos was overwhelming. Still, thanks to my wife's support, and encouragement from Robert F. Heizer and T. "Ted" D. McCown, I hung on. As a student, Heizer excavated with Hrdlička on Kodiak Island in

the 1930s, so we had a common interest in Alaskan anthropology. At the time, he was also involved with archaeological finds from Lovelock Cave in northwest Nevada. I wondered – could there be human dental information from the nonhuman artifacts? Hundreds of tule quids were an obvious source to search through. Bob let me examine a sample of 345 quids. I found surface impressions in 19.0 percent that were recognizable as human molar and premolar bite marks – the last crushing bite before the quid was discarded. I wrote a paper on these prehistoric bite marks, one that I am still proud of, so much so that it is part of the title of this contribution (Turner 1967).

Ted McCown was the departmental patriarch. This patrician elder, like Heizer, was a strong supporter. A few times a week he would stop in to visit me in my tiny top floor office that looked westward onto the San Francisco Bay. His interest was probably mostly professional, and not personal (he had been a dean, after all), because he made the final decision at the departmental level on my being hired at UCB, as he did earlier for Sherry Washburn and later for F. Clark Howell.

McCown casually interviewed me in the fall of 1962 at a student party in the Madison home of Bill and Ruth Laughlin, previously owned by W.W. Howell. Ruth had made delicious party food: huge hamburgers with all the fixings and lots of beer for the always-appreciative students. My task for the evening was to show slides of that summer's Aleutian and Kodiak field work. One slide was of a married Aleut couple embracing and kissing at an evening birthday party in their little house atop the 4,000-year-old Aleut village mound called Chaluka. The party had obviously started earlier in the day with the famous "Everclear," a 200 proof spirit flown in illegally to Nikolski Village. I had snapped the picture under poor, hand-held natural lighting, but it turned out remarkably well. I was the only one of our field crew invited to the little party, and between swallows of Everclear, I took as many photos as appropriate and as lighting permitted. When Ted McCown saw the sensuous slide, he immediately proclaimed it to be a picture of "mankind embracing woman," a pun on the then often-repeated phase, "anthropology is the study of man embracing culture." I still believe that candid photo helped me get the Berkeley job.

One semester, Don R. Brothwell was a visiting scholar from London. One of the pioneering publications that Don edited was the now-classic 1963 *Dental Anthropology*. We shared many common interests in dental anthropology and had a joint seminar on the subject. Among the seminar students was James D. Cadien, who would subsequently write his dissertation on the genetics of Carabelli trait. I resigned from UCB to take a research position at USNM, the purpose of which was to continue the New World physical anthropology studies conducted by Hrdlička. However, this did not work out, because just as a moving company was packing up our belongings, I got a call from Larry

Angel telling me President Johnson had frozen all new federal hires. I was a noncombatant casualty of the Vietnam War. But, by the end of summer 1966, I was hired again, this time back in Arizona, and with an additional daughter, Korri Dee.

2.3.5 Arizona State University, Tempe (ASU)

ASU would be my last institutional affiliation. It was here that Don Morris and I established a strong dental component to the graduate physical anthropology concentration. To help get our dental "program" off the ground by providing a resource for graduate student research, I agreed with a National Park Service proposal to curate the collection of human skeletal remains from the Globe regional center, which was being shut down. Most skeletons were excavated by Alden C. Hayes from Gran Quivira Pueblo in New Mexico. A preliminary osteological study of the remains had been conducted by Erik K. Reed. Around this time, Don Morris spent a year in South Africa duplicating dental casts of Bushmen, Bantu, and Asiatic Indians to bring back to ASU. He had previously collected dental casts of Papago Indians. In subsequent years cast collections were acquired from Hawaii (William Bass), the Solomon Islands (Howard L. Bailit), Easter Island (Stanley C. Skoryna, Alexander G. Taylor, and Robert J. Meier), the Batak, Philippines (James F. Eder), and Pima Indians.

The latter and largest cast collection had been assembled over a number of years by Al and Thelma Dahlberg. The story of how ASU acquired the "Dahlberg Collection" involves my having a late evening secretive meeting with Al and G.H.R. von Koenigswald in an old Mesa motel with little bungalows favored by Al and Thelma in their Arizona work. We discussed the pros and cons of donating the Pima collection to ASU Anthropology. Al and Thelma wanted the thousands of Pima casts and extensive genealogical records to be curated where the collection would be used for further local research. Since ASU was geographically near the Pima villages, and Don Morris and I were both working in dental anthropology, ASU was the natural place to house the collection. Following a ceremony of appreciation led by the liberal arts dean and an evening reception at the home of the department chair, Fred Plog, Roy Barnes traveled to Chicago to pack up the collection and move it to Tempe. The Pima collection has served as the basis for considerable regional and global research by graduate students, faculty, and visiting scholars.

A heterogeneous Euro-American collection was assembled during my tenure at ASU by taking dental impressions of all students who took my dental anthropology course, first taught in 1972. In my absence the course has been taught by B. Holly Smith and Diane E. Hawkey. Two other valuable dental cast

samples were collected by Lenore Fischer. Aided by Hispanic anthropology student Joe Katich, she made a number of dental impressions of Phoenix area Hispanics, the purpose of which was to help in my dental admixture research (Turner 1967). Lenore also traveled to Ireland, where, in small country villages, she collected impressions as part of her anthropological summer vacation. Odd as it may seem, taking dental impressions is much more understandable to "natives" than asking questions about religion, sexual practices, cannibalism, or other esoteric interests of anthropologists.

Some of my graduate students or I would spend part of several summer vacations collecting Hopi and Navajo dental impressions on the Hopi Reservation at the Keam's Canyon Indian Health Service Hospital. As in the Pima and Aleut-Koniag studies, we collected genealogical information on patients at the dental clinic. In every case, we asked the patient or parent whether we could take an impression for health, origins, and genetic research. The markedly cariogenic diet of both Hopi and Navajo individuals ensured a steady stream of clinic visitors.

Table 2.1 lists the ASU degree production in dental anthropology. Several theses and dissertations were based on ASU cast and osteological specimens. Table 2.2 lists the visitors who worked in dental anthropology. Several spent time in discussions with various students whose research interests were shared by the visitors.

2.4 Lifelong projects

2.4.1 Standardized reference plaques

Early in my ASU career, helped by Richard Scott, I began a Wenner-Gren-supported project of making plastic plaques for the standardized scoring of specific intratrait variation. The first ASU plaques were ranked scales for lower first permanent molar cusps 6 and 7. Previously published articles suggested these two traits might serve as valuable features for characterizing Africans (high percentage cusp 7), Europeans (low percentage cusp 6), and Asian-Native Americans (high percentage cusp 6). Much variation of both cusps 6 and 7 can be easily recognized, even when occlusal wear is marked, as it usually is in archaeological-derived collections. We selected examples from our cast and osteological collections of total absence (0) and equally spaced grades of expression of increasing size from 1 to 5 (faint to pronounced). Unlike the descriptive system of crown groove patterning developed by Alexander A. Zoubov that he called "odontoglyphics," which works best with unworn teeth of children, the Arizona State University Dental Anthropology System

Table 2.1. *Arizona State University student research in dental anthropology*

1. Nancy T. Morris (1970) MA, *The occurrence of mandibular torus at Gran Quivira*
2. G. Richard Scott (1973) PhD, *Genetic analysis of American white families and variation in living Southwest Indians*
3. Mahmoud Y. El-Najjar (1973) PhD, *People of Canyon de Chelly, a study of their biology and culture*
4. Cheryl E. Swanson (1976) MA, *Dental pathologies in Gran Quivira*
5. Edward F. Harris (1977) PhD, *Anthropologic and genetic aspects of the dental morphology of Solomon Islanders, Melanesia*
6. Dennis J. Ryan (1977) PhD, *The paleopathology and paleoepidemiology of the Kayenta Anasazi Indians in Northeastern Arizona*
7. Meredith A. Larson (1978) MA, *Dental morphology of the Gran Quivira Indians*
8. Jeffrey C. Long (1978) MA, *Microstructural defects in the dentin*
9. Michael S. Boyce (1979) MA, *The thickened tympanic plate*
10. Sheila Coyne (1981) Mandibular first premolars of Gran Quivira. In *Contributions to Gran Quivira Archeology*, A. C. Hayes, ed. Pp. 139–140, National Park Service, Washington, D.C.
11. Kenneth R. McWilliams (1981) Non-metric oral traits in Gran Quivira skeletons. In *Contributions to Gran Quivira Archeology*, A. C. Hayes, ed. Pp. 147–149, National Park Service, Washington, D.C.
12. Betty J. Schmuker (1983) MA, *Dental attrition: a comparative study of dietary and subsistence patterns*
13. Alice "Sue" Haeussler (1985) MA, *Dental morphology of New World, Eastern Siberia, and Soviet Central Asia populations*
14. Lanitta Collette Van Nimwegen (1989) MA, *Labret use among Arctic and Subarctic peoples*
15. Christian R. Nichol (1990) PhD, *Dental genetics and biological relationships of the Pima Indians of Arizona*
16. Alison Kadlic Donta (1992) MA, *Dental caries and diet in turn-of-the-century Pima population from the Maricopa Road site AZT1688*
17. Kathy L. Roler (1992) MA, *Near Eastern dental variation past and present*
18. Joel D. Irish (1993) PhD, *Biological affinities of Late Pleistocene through modern African Aboriginal populations: the dental evidence*
19. Edwin F. Crespo (1994) MA, *Dental analysis of human burials recovered from Punta Candelero: a prehistoric site on the Southeast coast of Puerto Rico*
20. Esther E. Morgan (1994) MA, *Tooth wear in modern Hopi Indians*
21. Erin Cacciatore (1994) MA, *The etiology and worldwide distribution of interproximal grooving of human teeth*
22. Shara E.Baily-Schmidt (1995) MA, *Population distribution of the tuberculum dentale complex and anomalies of the maxillary anterior teeth*
23. Alice "Sue" M. F. Haeussler (1996) PhD, *Dental anthropology of Russia, Ukraine, Caucasus, Central Asia: the evaluation of five hypotheses for Paleo-Indian origins*
24. Joshua G. Lipschultz (1996) MA, *Who were the Natufians? A dental assessment of their population affinities*
25. Jaimin D. Weets (1996) MA, *The dental anthropology of Vanuatu, Eastern Melanesia*
26. Diane E. Hawkey (1998) PhD, *Out of Asia: dental evidence for microevolution and affinities of early populations from India/Sri Lanka*
27. Scott E. Burnett (1998) MA, *Maxillary premolar accessory ridges (MXPAR): worldwide occurrence and utility in population differentiation*

(*continued*)

Table 2.1. (*cont.*)

28. Lorrie Lincoln-Babb (1999) MA, *The dental morphology of the Yaqui Indians: an affinity assessment*
29. Christine Lee (1999) MA, *The origins and interactions of the Caddo Indians: a study in cranial and dental nonmetric traits*
30. Alma J. Adler (1999) MA, *The dentition of contemporary Finns*
31. Stephen C. Reichardt (2000) MA, *The Woodland Iroquoian people of Southern Ontario: a dental assessment of their population affinity*
32. Anna Konstantatos (2000) Publishable Paper (MA alternative), *Dental health and disease at the Roman-era site of Fiskardo on the island of Cephalonia, Greece*
33. Jaime M. Ullinger (2002) MA, *A dental reconstruction of biological relationships in the Late Bronze–Early Iron transition of the Southern Levant using dental morphological traits*
34. Shara E. Bailey (2002) PhD, *Neandertal dental morphology: implications for modern human origins*
35. Alma J. Adler (2005) PhD, *Dental anthropology in Scottland: morphological comparisons of Whithorn, St. Andres and the Carmelite Friaries*
36. Cassandra L. Kuba (2006) PhD, *Nonmetric traits and the detection of family groups in archaeological remains*
37. Christine Lee (2007) PhD, *The biological affinities of Neolithic through modern period populations from China and Mongolia: the cranial and dental nonmetric evidence*

Table 2.2. *Visiting dental scholars to ASU*

Albert A. Dahlberg, University of Chicago (April 9–13, 1979; February 20–26, 1983; March 18–20, 1985). Pima records. Donation of Pima cast collection.
C. Loring Brace, University of Michigan (December 9–11, 1979). Metric data collection, lecture.
B. Holly Smith, University of Michigan (Fall 1983). Teach dental anthropology course and collection of wear data.
William S. Laughlin, University of Connecticut (January 19–March 23, 1985). Lectures and Aleut dentition.
Simon Hillson, University College, London (March 25–28, 1985). Lecture, enamel defects.
Joseph B. Birdsell, UCLA (April 1–24, 1985). Lectures, Australian dental clines.
Kazuro Hanihara, University of Tokyo (May 1985). Lectures, Japanese and Ainu dentition.
Stephen Molnar, Washington University (December 15–16, 1986). Wear data collection.
Liu Wu (Fall–Spring, 1991–92) Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing. Attend dental anthropology classes, ASUDAS.
Alexander A. Zoubov, Institute of Ethnography, Moscow (November 25–26, 1991). Lectures.
Daris R. Swindler, University of Washington (April 3–5, 1995). Lecture.
Tasman Brown, University of Adelaide, Australia (April 3–5, 1995). ASUDAS.
Yoshitaka Manabe, Nagasaki University, Nagasaki, Japan (Fall–Spring, 1999–2000). Attend dental anthropology classes, ASUDAS.
Alfredo Coppa, Rome (1992). ASUDAS.
Cleber B. Periera, Uruguaiana, Brazil (dates not recalled) Yanomama dentition.

(ASUDAS) was intended to extract as much information as possible from often very worn archaeologically-derived teeth.

This program refined and added to the plaques developed by Dahlberg. Students taking my dental anthropology course were encouraged to do their term projects by identifying new traits in our collections, especially those whose frequencies varied among groups, and to develop plaque prototypes. These new standards are identified and defined in Turner, Nichol, and Scott (1991). We never added to or refined the series of deciduous crown plaques developed by Kazuro Hanihara when he was studying with Dahlberg at the Zoller Dental Clinic in Chicago. The ASUDAS has been widely adopted around the world. The older Dahlberg plaques are rarely used anymore, and the Zoubov odontoglyphic system is used today only in Russia and former Soviet states.

2.4.2 Peopling of the Pacific Basin and adjoining areas

A second project on the peopling of the Americas and Pacific produced about forty papers, not all of which have been published. I traveled throughout the New World, the Pacific, eastern Asia, and Siberia to collect the needed observations. I studied museum and institutional collections in Canada, the United States, Mexico, Ecuador, Peru, Chile, Brazil, Australia, Thailand, Philippines, Hong Kong, Taiwan, Japan, England, France, Netherlands, Denmark, Estonia, and Russia. Many of these European institutions had human skeletal collections that originated in the Asia-Pacific realm. For example, the original ancient Brazilian Lagoa Santa skeletons, found by the Danish geologist P. Lund, are curated in the Copenhagen Zoology Museum.

By the time I stopped making observations because of failing vision, there were about 30,000 individuals in the database; the latter included comparative observations of European teeth taken in London, Paris, Utrecht, Copenhagen, Moscow, St. Petersburg, Tallinn, and Novosibirsk. My wife, Jacqueline, and daughter Korri Dee helped collect much of the data. Linda Nuss Watson and Rhea Jacanin did all computer data entry and ran all statistical programs. Assembling the database and its subsequent analyses was aided by grants from NSF, IREX, U.S. and Russian Academies of Science, National Geographic Society, Wenner-Gren Foundation, and my ASU Regents' Professor research account; I also made a few observations on collections that originated from Sudan, West Africa, and South Africa. Joel D. Irish has since provided most of the African observations employing the ASUDAS (see chapter 12, in this volume). I came across a small series of South Asians in an Australian museum, but most of what we know about India and Sri Lanka using the ASUDAS is from the work of Diane Hawkey. As mentioned, my wife and youngest

daughter helped with much of the worldwide data collecting. I recall my surprise in 1991 to see Korri Dee one day walk into Sydney University's N.W.G. Macintosh Anatomical Museum where Jackie and I were collecting dental data from a large collection of Australia Aborigines. She arrived on Father's Day as a surprise, which it certainly was. This trip took us to Brisbane, Sydney, Canberra, and Adelaide, where we met Tasman Brown; his charming wife, Kerry; and his well-known dental associates.

2.4.3 The dental morphology of anatomically modern humans

A third project grew out of the second. It was aimed at establishing dental characteristics of modern and recent human populations with an aim to see whether microevolution, affinity, and dispersals of modern populations could be reconstructed. This work culminated in a book on worldwide variation in dental morphology entitled *The Anthropology of Modern Human Teeth: Dental Morphology and Its Variation in Recent Human Populations* (Scott and Turner 1997). We recognized five major modern dental populations: Western Eurasia (including North Africa and India), sub-Saharan Africa, Sino-America, Sunda-Pacific, and Sahul-Pacific. These divisions have substantial correspondence with linguistic, archaeological, genetic, and ethnographic classifications.

2.4.4 Genetics and microevolution

This interest is reflected in my 1967 dissertation and dissertations by Richard Scott, Edward Harris, and Christian Nichol. Among modern populations, genetic drift and gene flow are the major evolutionary processes affecting the dental characteristics of many groups (Turner 1969). The best case we have for a dental morphology mutation is shown in an upper first premolar variant that Don Morris called the Uto-Aztecan premolar. Human genetics interests were shared with ASU geneticist Charles M. Woolf, who helped finance the PhD programs of Scott and Harris and served on their graduate committees.

2.4.5 Environmental effects

Included here are all the natural and cultural factors that can affect teeth. Natural factors include wear caused by foods contaminated with abrasives and accident risks in environments such as slippery coastal shorelines or rocky terrains – where falls can result in fractured teeth. Such fractures can also occur

in the cultural domain where conflict is common. Unintentional effects include labret faceting, interproximal grooves, and chipping when teeth are used as an aid in tool production. Intentional modification includes filing and incising of various types and extraction or ablation. Several students have prepared theses in this domain (Table 2.1).

There are scores of people who helped me in many ways throughout my student and professional life. The number is too large to repeat here, but the many helpful curators, administrators, museum assistants and associates, students, archaeologists, physical anthropologists, and cultural anthropologists are acknowledged in various articles published for this and two other long-term projects.

2.4.6 Other ideas

There are projects I never got around to. I wanted to do a descriptive and microevolutionary study on sea otter teeth (my Aleutian experience) and a similar study of hyena teeth (Siberian experience). I have pondered why early Southwest Indians had relatively big teeth, while later people had smaller teeth. Why did modern Inuit (and other Eskimo) have such a high frequency of congenitally missing third molars in light of their dentally demanding environment? What caused dental reduction of Upper Paleolithic Europeans relative to the large teeth of East Asians who lived in the same sort of late Pleistocene environment and had similar dentally related cultural equipment? Perhaps graduate students or professional colleagues will tackle these fascinating issues in the future.

2.5 Conclusion

In sum, my main interest in dental anthropology has been to use crown and root morphology as an independent means of solving anthropological problems, especially those involving the origins and dispersal of anatomically modern humans. The central problem has always been colonization of the Pacific Basin and surrounding areas – the Americas, Oceania, and East Asia, including Siberia. This approach is much like that used in linguistics and employed one of that discipline's major assumptions, that is, similar languages must be related. Hence, groups with similar dental morphology must be more closely related than those with dissimilar teeth. Implicit is the recognition of fast or slow microevolution depending on population size and structure, and environmental conditions. Also, like words, dental morphology must be largely

inherited. In my view, intergroup differences in secondary dental morphology, such as cusp number, were caused mainly by genetic drift/founders effect, whereas primary features, such as tooth groups (incisors, etc.), are controlled by natural selection. Northeast Asian Sinodonty must have evolved out of Southeast Sundadonty at least 15,000 years ago because all past and present Native Americans are Sinodonts, the earliest of whom crossed Beringia around 15,000 years ago. Microevolution must have been caused by genetic drift because Sinodonts have probably occupied northern Eurasia as long as did Cro-Magnons. The dentitions of the two are strongly dissimilar, yet they lived in a nearly identical environment and with similar tool technologies as far as teeth are concerned.

In closing, I sense that the definition of dental anthropology has broadened considerably since I first saw excavated human remains at Point of Pines in 1955. Proof of this can be seen in the emergence of the journal *Dental Anthropology* with its diversity of articles that appear in every issue as well as, morphologically speaking, the chapters that follow in this volume.

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3 *Twin and family studies of human dental crown morphology: genetic, epigenetic, and environmental determinants of the modern human dentition*

TOBY E. HUGHES AND
GRANT C. TOWNSEND

3.1 Introduction

In Scott and Turner's (1997) *The Anthropology of Modern Human Teeth*, a significant portion of the fourth chapter explores the concept that many nonmetric dental crown features are determined by genetic factors acting during odontogenesis; hence, they provide reasonable proxies for inferring evolutionary change in human populations. Key early work by researchers including Kraus (1951), Moorrees (1962), Garn (1977), and Harris (1977) explored simple Mendelian, quasi-continuous, and polygenic models of crown variation for nonmetric traits. Here, we seek to provide an update of current knowledge regarding the degree of genetic influence on variation in many crown features used commonly to infer evolutionary trends, with particular reference to our research on Australian twins. We extend earlier work by examining both nonmetric and metric dental data, and by considering both multivariate models of phenotypic data and the integration of molecular genetic data into models of crown variation.

3.2 Background

The dentition has a number of special or unique features that make it an excellent system from which to develop and test ideas about early development

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in individuals and to examine change through time within populations. Development of the dentition is initiated during embryogenesis around 6 weeks *in utero* but is not finalized until young adulthood; thus, it is useful as a means to examine the role of environment in development over time. Each tooth passes through a series of developmental stages that follow the same pattern, commencing with formation of the tooth bud, followed by the cap and bell stages of development, then by laying down of enamel and dentine over the tooth crown. Root development follows, with the tooth emerging into the oral cavity when around two-thirds of the root has formed. The morphology of each crown is fixed post calcification, and thus acts as a permanent record of environmental perturbations during development.

Morphologically, the dentition exhibits structure at multiple levels, from the organization of cusps on a molar crown, to integration of tooth classes within a quadrant, to complex occlusal relationships between teeth of the maxilla and mandible. Many of these features are (relatively) straightforward to quantify with a high degree of precision and accuracy, and methodologies for doing so have been reported (Brook et al. 1983, 1999; Smith et al. 2009). The dentition is bilateral, a structure that enables the roles of genes and environment in the development of asymmetry (both fluctuating and directional) to be examined. There is growing evidence that the dentition satisfies the requirements of a complex system, in which lower-level, interacting components give rise to higher-level, emergent phenomena. The system is composed of a hierarchical organization of functional subunits, including cells, tissues, organs, and, if the concept is taken to its logical end point, organisms and populations. This "self-adaptive" system has the capacity to react to change through time, within an individual and transgenerationally (Brook and O'Donnell 2012).

The human dentition demonstrates significant variation in development, form, and function. This variation exists within and between individuals, families, sexes, ethnic groups, and populations. It has been attributed to temporal effects acting at the level of the individual (within a lifetime) and at the level of the population (across generations). Development of the crown reflects environmental and epigenetic modulation of gene expression through time. All disciplines stand to benefit from a better understanding of the genetic, epigenetic, and environmental factors that play a significant role in odontogenesis, giving rise to the broad variation in form and function observed within and between dentitions in modern humans.

Questions of interest include "How does plasticity of the genome give rise to dental crown adaptation within populations to a particular environment?" and "Which genes play a significant role in the development of a specific dental crown phenotype?" These questions can be addressed using family studies: that is, the former through use of population modeling of traits that exhibit

familial aggregation and the latter through use of linkage and association analyses to elucidate the role of specific genes in trait development. More recently, the role of the epigenome in dental development and patterns of trait transmission has generated interest among dental anthropologists. This aspect, too, can be addressed through the judicious use of family data.

Studies of twins and other familial relationships have much to offer in terms of a first-pass examination of the likely role of genes and/or the environment in crown development and the relationships between crown-specific variables. More recently, data sets from family-based approaches have been used to establish links between observed phenotypic variation and putative genetic loci. Twin data sets are particularly useful for whole-genome approaches to associate phenotype with the genotype, as they eliminate issues associated with population stratification common in case-control designs.

Over the past 25 years, our group has developed a large collection of dental records from a series of Australian twin family cohorts, with many of the records being longitudinal in nature. We also have significant collections from a number of distinct ethnic groups. This chapter provides a summary of key findings published by our group and others on genetic and environmental factors that play a significant role in morphological variation of the modern human dental crown.

3.3 Embryology

Embryogenesis of the human tooth has been exhaustively documented elsewhere (e.g., Nanci et al. 2003). The key developmental features of odontogenesis are illustrated in Figure 3.1. Similar to many other structurally important organs, odontogenesis involves a complex interaction between epithelial and mesenchymal tissues. This interaction is initiated and controlled by a cascade of genes and gene products, leading to an acquisition of form and function that is, under normal circumstances, tightly controlled spatially and temporally.

Molecular biology has provided a comprehensive picture of the processes involved in odontogenesis, including the development of crown shape (Sperber 2004; Tucker and Sharpe 2004). Folding of the internal enamel epithelium, which represents the future dentinoenamel junction and provides a blueprint for the morphology of completed crowns, is determined by a series of reciprocal interactions between epithelial and ectomesenchymal tissues. This folding is associated with the appearance of nondividing groups of cells, referred to as enamel knots. These knots act as signaling centers, producing and responding to various local activating and inhibiting molecules. The primary enamel knot seems to be an important regulator of overall tooth shape during the cap stage

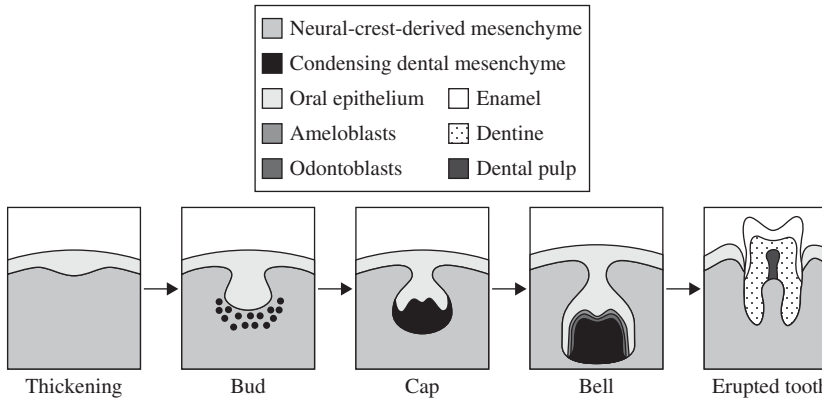

Figure 3.1. Odontogenesis.

of odontogenesis (Jernvall and Jung 2000), and secondary enamel knots form subsequently at the sites of future cusp tips. Clearly, there needs to be some control of spacing of the secondary knots as this determines future cusp position (Jernvall and Thesleff 2000); however, our studies of intercuspal distances indicate that considerable variability can occur in these dimensions (Townsend et al. 2003). Development of individual cusps appears to use the same set of developmental genes repeatedly, forming a so-called developmental module; it is thought that the repeated activation of these developmental modules may explain the cumulative variation of later-developing cusps (Jernvall and Jung 2000; Salazar-Ciudad and Jernvall 2003).

3.4 Aspects of variation in dental crown morphology

Although highly conserved in an evolutionary context, basic embryological processes associated with tooth development are subject to genetic and environmental influences that give rise to variation at various organizational levels within modern humans, including:

- within a tooth (cusp size and position; mesiodistal versus buccolingual dimensions)
- between right and left antimeres, and upper and lower isomeres
- between teeth within a class (central versus lateral incisors)
- between tooth classes (canines versus molars)
- between dentitions (primary versus permanent)
- between family members, genders, ethnic groups, populations, and generations

The dental crown demonstrates a range of morphological variation both within and between individuals and populations. This variation can occur at the level of the whole tooth or may be limited to particular aspects of the crown. There are many aspects of the dental crown that have been examined repeatedly in the literature. Some common variables include those that vary in a continuous manner, such as measures of linear dimension, surface contour, area, and volume; others take discrete values or scores, such as the presence or absence of teeth, presence and expression of extra cusps (e.g., Carabelli trait), shape of grooves on the occlusal surface, and presence and/or expression of a range of discrete morphologies (e.g., shovel-shaped incisors, lingual tubercles, etc.). It should be noted that, for the most part, whether a crown characteristic is considered a binary, discrete, ordinal, continuous, or interval-scale variable, it is often dependent on limitations of the measurement tool, or preference of the examiner. It should also be emphasized that many traits show significant covariation, a likely consequence of their shared developmental trajectory. Although tooth crowns show a degree of variation in size and shape, there is a fundamental allometric relationship among teeth within the dentition; dimensional traits (size, area, volume) or those that may be influenced by dimensional thresholds (e.g., tooth number, molar cusp number) are likely to be highly correlated phenotypically. This relationship is important to consider when drawing inferences about factors associated with dental development; generally, multivariate approaches are preferred when many (possibly correlated) phenotypes are available.

Various methods have been used to quantify human dental crown variation as a means of examining population affinities. Traditionally, this approach entails visual scoring of nonmetric characteristics or using calipers to quantify linear dimensions. New technologies such as two-dimensional and three-dimensional imaging now provide alternatives to exploit more robust approaches, including the gamut of geometric morphometric tools.

3.5 Variation in the timing of dental development

Human teeth exhibit heterodonty, meristicity, bilateral symmetry, and a phased temporal replacement of primary with permanent teeth. Therefore, control of developmental timing requires tight regulation to ensure allometric growth trajectories give rise to a functional dentition that is stable throughout life. Morphogen gradients in embryogenesis and the role of an odontogenic homeobox gene code have both been implicated in the control of odontogenesis timing.

Over the past several decades, work with animal models (e.g., Thesleff 2006) has provided information on the reiterative processes governing development

of the enamel crown that allow for variation of morphology within the patterned dentition. More recent work (e.g., Salazar-Ciudad and Jernvall 2002) has gone into the creation of simulated models of dental development that indicate how regulatory cascades of gene action give rise to final morphologies. These models can be used to explore how subtle shifts in timing and/or degree of gene action can give rise to morphological variation within and between individuals of the same and different species, both extinct and extant. These models are now being tested through *in vivo* models of animal dental development.

3.6 Dental crown patterning

There are qualitative differences in crown form anteroposteriorly, a result primarily of dietary requirements modulating tooth form during modern human evolution. What gives rise to the well-defined and highly conserved patterns of dental crown groups in the human dentition? The concept of morphogenetic fields within the dentition was first proposed by Butler (1939), and then adapted for the human dentition by Dahlberg (1945, 1951). An alternative clone theory of dental development was proposed by Osborne (1978). More recently, Sharpe (1995) put forward the concept of an odontogenic homeobox code to explain how different tooth classes are initiated in the oral cavity in response to molecular cues and the expression of specific groups of homeobox genes. Certain genes may act on multiple dental phenotypes pleiotropically. These are commonly homeobox-like genes that regulate expression of structural genes and often play a role reiteratively during development. The complex relationships among these genes are now thought to give rise to developmental fields within the human dentition. The odontogenic homeobox code model explains how dental patterns can be generated from different domains of expression of homeobox genes in neural crest derived ectomesenchyme (Osborne 1978; McCollum and Sharpe 2001).

Mitsiadis and Smith (2006) proposed that the field, clone, and homeobox code models could all be incorporated into a single model to explain dental patterning. The authors provide a schematic representation of how patterning can be produced by an odontogenic homeobox code. They describe how an "intermixing" of genes expressed by ectomesenchyme of the first branchial arch can lead to establishment of different morphogenetic fields. Patterns are established by signals from the ectoderm that induce specific domains of homeobox gene expression in the ectomesenchyme. This patterning is plastic initially but over time becomes fixed into the "memory" of the ectomesenchymal cells. It

is these specific domains that are postulated to provide molecular information needed to specify different tooth shapes (Cobourne and Mitsiadis 2006). Townsend et al. (2009) provide a comprehensive review of these theories in the light of findings from molecular, cellular, genetic, theoretical, and anthropological investigations; they agree that these three models should be viewed as complementary rather than contradictory and propose that this unifying view could be extended to observations of dental patterning in individuals with missing and extra teeth. The authors note all three theories are compatible with the unifying etiological model of crown development based on human epidemiological and clinical findings developed by Brook (1984).

There is evidence that the nature of molecular signaling in the upper and lower jaws may vary. The dental formula is the same in both arches in mice and humans, but the shape and morphologies of homologous teeth in the two jaws are distinctive, one from the other (Cohn 1957). Biochemical signaling differences have been demonstrated in the mouse for *Dlx* genes (Thomas et al. 1997; Depew et al. 2002) and for activin/follistatin (Ferguson et al. 2001); however, it is not known how neural crest-derived cells migrating into the developing maxillary and mandibular regions develop the ability to respond differently to ectodermal signaling. Reports of apparently independent genetic determination of maxillary and mandibular dentitions, based on tooth-size data derived from twins (Potter et al. 1976), are consistent with the molecular evidence.

3.7 Nonmetric and metric dental traits

Many dental anthropologists have focused on nonmetric traits to characterize major populations (Hanihara 1967; Scott and Turner 1997). On the basis of such traits, various "dental complexes" have been identified, including Mongoloid, Caucasoid, Negroid, and Australoid (Mayhall et al. 1999; Turner 1990; Townsend et al. 1990; Irish, this volume).

In conjunction with nonmetric traits, odontometric variation has also been used in the investigation of human populations (Falk and Corruccini 1982; Hanihara 1998; Hanihara and Ishida 2005; Kieser and Groeneveld 1991). On the basis of these studies, populations have been grouped as microdontic, mesodontic, and megadontic (Harris and Rathbun 1991). Some researchers have claimed that nonmetric traits are more useful than continuous characteristics in grouping people by geographic location and affinities (Hanihara 2008; Lasker and Lee 1957). Measurements of crown and arch size, however, provide greater objectivity than scoring of traits. A combination of metric and

nonmetric features is likely to provide the most comprehensive and discriminatory description of human dentitions.

3.8 Environmental factors

There is ample evidence from the literature outlining the role of environment in variation in crown morphology among individuals. Examples include trauma to teeth, either before or after emergence; systemic infections or illnesses that affect deposition of mineralized tissue, leading to enamel hypoplasias; and tooth wear due to tooth-to-tooth contact (attrition), abrasion caused by exogenous substances, or erosion due to intrinsic or extrinsic acidic substances. It is beyond the ambit of this chapter to explore the various specific environmental factors, other than to acknowledge that many of our genetic models in twins suggest at least some degree of environmental influence on most dental morphological features, most probably associated with effects on size and allometry.

3.9 Genetic factors

More than three hundred genes have been identified as playing a role in odontogenesis, with many related to cellular communication (Thesleff 2006). Some genetic signaling pathways involved in this communication include *Fgf*, *Bmp*, *Shh*, *Wnt*, and *Tnf*. Reciprocal interactions between the ectodermal and ectomesenchymal tissues regulate key stages in the process of odontogenesis, including initiation, morphogenesis, and differentiation.

The role of the genome in dental crown variation is similar to that of many human conditions. A number of features are influenced by only one or a few genes and these show a simple pattern of inheritance. They are most commonly disease states and may be the result of specific allelic variants "tipping" an individual over a phenotypic threshold in the presence of a polygenic background (Brook 1984).

Variations in most dental features of interest are due to the additive effects of many genes and/or environment (classical heritability). Other effects may complicate the outcome, including allele interactions at the same locus (e.g., genetic dominance), allele interactions between loci (e.g., epistasis), and interaction of genes with their environment (e.g., epigenetics). Significant phenotypic correlation observed between many dental features also indicates a role for the pleiotropic influences of genes or environmental factors. Such complex traits characteristically show a distribution (most commonly normal) within a

population and can be considered multifactorial. These features provide the most challenge to elaborate etiologically.

3.10 Epigenetic factors

Canalization is a measure of the ability of a population to produce the same phenotype regardless of variability of its environment or genotype (Waddington 1942). Canalization comes about when developmental pathways are shaped by evolution. Waddington (1942) introduced the concept of the epigenetic landscape, in which the state of an organism rolls "downhill" during development. In this metaphor, a canalized trait is illustrated as a valley enclosed by high ridges, safely guiding the phenotype to its "fate." The author claimed that canals form in the epigenetic landscape during evolution, and that this heuristic is useful for understanding the unique qualities of biological robustness. Holliday (1990) further refined the definition of epigenetics as "the study of the mechanisms of temporal and spatial control of gene activity during the development of complex organisms." Thus "epigenetic" can be used to describe anything other than the deoxyribonucleic acid (DNA) sequence that influences the development of an organism.

In the last 10 years, there has been an increasing focus on the interface between the genetic code and an individual's environment. Increasingly, evidence suggests the epigenome plays a significant role in the adaptation of an individual's genome to environmental factors. Molecular mechanisms that have been implicated include DNA methylation, histone deacetylation, and the role of micro ribonucleic acids (RNAs) in gene expression. There is growing evidence that epigenetics plays a role in dental crown development, particularly how the homeobox code regulates pattern formation in embryogenesis. We postulated recently that minor variations in so-called epigenetic events during odontogenesis may account for distinct differences in expression of missing and extra teeth in our sample of monozygotic (MZ) twins (Townsend et al. 2005). Drawing on the work of Molenaar et al. (1993), we proposed that the process of odontogenesis represents a good example of a developmental system with emergent self-organizing properties; in this system, minor variations in local epigenetic events may lead to major differences in phenotypic expression between MZ co-twins, even though they are presumed to be identical genetically. Our group is exploring the influence of the epigenome on differences in the dentitions of MZ twin pairs. In the first instance, we are examining the possible role of differential methylation patterns (whole-genome and candidate-gene) on discordance between MZ co-twins in the expression of agenesis and/or extra teeth. It is important to realize there are many reasons why MZ

co-twins differ, with Martin et al. (1997) providing a comprehensive summary of pre- and postnatal genetic and environmental influences that potentially lead to phenotypic and genotypic divergence.

3.11 Modeling dental crown morphological variation

Studies of complex traits showing familial aggregation provide one means to identify putative etiologic agents. In this regard, quantitative genetics is complementary to the domain of the molecular biologist, seeking to provide a framework of genetic variation within which models of specific gene action can be located. Together, the disciplines provide an opportunity to understand better the interplay between components of complex systems. Quantitative genetics relies on the development of theoretical models from a sound understanding of the biological system under analysis. These models may then be validated by real-world data, often using likelihood-based approaches. This approach requires the collection of both intensive and extensive phenotypic data to substantiate the conceptual model. We have suggested the term "dental phenomics" to describe this comprehensive approach to phenotyping the human dentition (Townsend et al. 2012).

A key feature of quantitative genetic analysis in humans is a reliance on known or inferred familial relationships. Knowledge of these relationships, and the transmission of alleles via meiosis, enables the dental anthropologist to develop models of trait transmission that predict the phenotypic outcome of genes segregating in families. The models are then compared to observed trait transmission in the same families to estimate goodness of fit. Genetic modeling is methodologically robust and provides a framework within which to locate evidence of gene effects from modern, high-throughput genotyping approaches. The twin family structure is particularly well-suited to this approach and provides a number of advantages analytically, particularly in the presence of population stratification.

3.12 Twin and family studies

The modern history of twin studies derives from Galton's (1875) pioneering use of twins to study the role of genes and environment in human development and behavior. Galton, however, was unaware of the critical genetic difference between monozygotic and dizygotic (DZ) twins. Crow (1999) notes that by 1910, Wilhelm Weinberg used the MZ-DZ distinction to calculate their respective rates from ratios of same- and opposite-sex twins in a maternity population,

worked out partitioning of covariation among relatives into genetic and environmental elements (anticipating Fisher and Wright) – including the effect of dominance on relatives' similarity – and began the first classic twin studies.

The power of twin designs arises from the fact that twins may be either monozygotic (from a single fertilized egg and sharing all alleles) – or dizygotic (from two fertilized eggs and sharing *on average* 50 percent of their polymorphic alleles, the same level as nontwin siblings). These differences in genetic similarity, together with a testable assumption of equal environments for MZ and DZ twins (Bouchard and Propping 1993), creates the basis for the twin design that enables exploration of the effects of genetic and environmental variance on a phenotype (Neale and Cardon 1992).

3.13 The classical twin design

Classical twin studies involve comparing features of interest in large numbers of MZ twin pairs with those in DZ twin pairs. Assuming that environmental influences are the same in both groups, greater similarity between MZ twin pairs compared with DZ twin pairs indicates that genetic factors are contributing to observed variation. The basic logic can be understood with little mathematics beyond an understanding of correlation and the concept of variance. The classic twin study begins from assessing variance of a phenotype in a large group and attempts to estimate how much is due to genetic effects (heritability) versus that due to shared or unique environmental effects – events that affect each twin in a different way or one twin but not the other. Typically these components are called A (additive genetic), C (common environment), and E (unique environment) – the so-called ACE model. It is also possible to examine nonadditive genetics effects (often denoted D for dominance in an ADE model).

Figure 3.2 presents a simple path diagram of a structural equation model (SEM) representing the twin relationship for a single trait. Variation in the observed twin phenotypes (square boxes) is influenced by a number of latent (unmeasured) variables (circles). Broadly speaking, these are the additive effects of an individual's genes (A), nonadditive effects (dominance, epistasis) of an individual's genes (D), influence of the environment shared by co-twins (C), and unique environment experienced by an individual twin (E). This last variable also encapsulates experimental error. The model completely decomposes observed variation into a number of discrete linear relationships between latent and measured variables, related by a series of parameters (a, d, c, e) that can be estimated using likelihood-based approaches. "Structural" elements of the model (intrapair correlations, r) capitalize on the observer's knowledge of

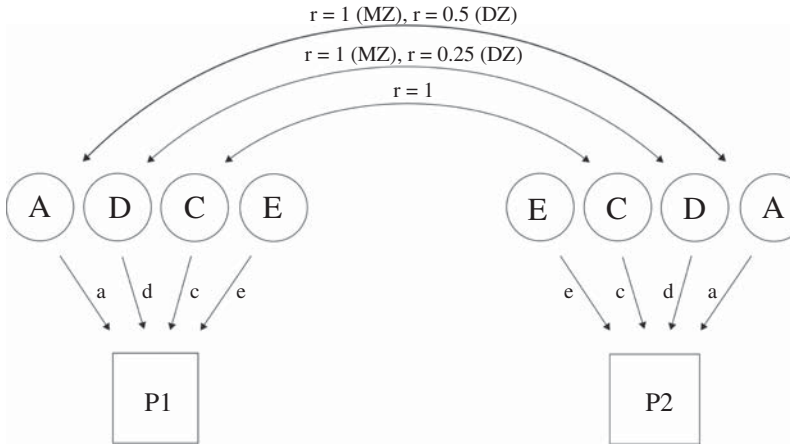

Figure 3.2. A univariate path diagram of the twin relationship.

biology underpinning the relationships *between* latent variables. To this end, additive genetic effects have a correlation (r) of 1 in MZ twins, and 0.5 in DZ twins; unsurprisingly, correlation between shared environments is 1 regardless of zygosity – twin pairs experience the same shared environment.

Given a well-fitting phenotypic model, researchers can determine what proportion of variance in a trait is heritable, compared to the proportions that are due to nonadditive gene effects, shared environment, or unshared environment. The essential logic of the twin design is as follows: given an observed covariance matrix from raw data, parameter estimates for the model are derived using a multinomial implementation of the likelihood function, maximizing the likelihood iteratively to produce a model that best approximates real-world data (with judicious use of good starting values). Structural equation modeling software such as Mx (Neale et al. 2003), now implemented in R (R Development Core Team 2011), is ideal for this purpose. Invariably, models of this nature fit well, being essentially a transformation of the data. The focus then switches to whether simpler models may also fit the data without a significant decrease in model fit. Simpler models can be compared to more complex models using appropriate statistics or information criteria to reach the most parsimonious explanation of the observed data (Neale and Cardon 1992).

The preceding univariate model can be extrapolated to the multivariate case to answer more explicit questions regarding data structure: (1) Do genetic effects change through time? (2) Is there sexual heterogeneity for trait variance? and (3) Are there pleiotropic influences of individual genes? Figure 3.3 illustrates a multivariate model of mesiodistal size of all incisors in the primary dentition of a cohort of Australian twins (Hughes et al. 2005). Variation

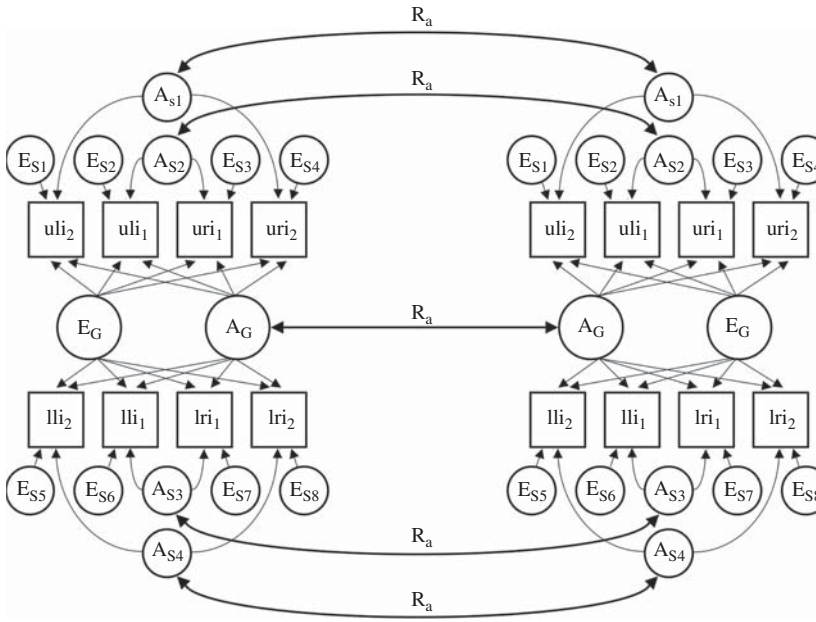

Figure 3.3. A multivariate path diagram of the mesiodistal dimension of primary incisors of Australian twins.

in primary incisor size is best described by a model incorporating a single general genetic effect on all teeth (A_G), as well as specific genetic factors for each set of antimeres (A_{S1}–A_{S4}). Of note is the increased complexity of the covariance structure relative to the univariate case. Figure 3.4 illustrates a longitudinal model of arch shape in the same cohort. The simplex model for longitudinal data allows for innovation elements at each time point (ζ_g, ζ_e) and directional transmission elements between time points (β_g, β_e), as well as an estimate of experimental error (ε, constrained equal across time) that is now independent of unique environmental effects, E_i. Factor loadings (λ) are fixed at 1 for model identification. This model allows for genetic elements acting at discrete timepoints, as well as transmissible genetic elements that account for variation through time.

One of the appeals of structural equation modeling is that it is flexible enough to enable incorporation of molecular genetic data to establish the putative influence of key genes. This is true regardless of whether one is using a genetic linkage-based approach or genetic association–based approach. These methods emphasize the utility of familial data for modeling gene action. Linkage analysis, by definition, requires information on the cotransmission of traits and genetic markers between family members, and hence relies on family-based

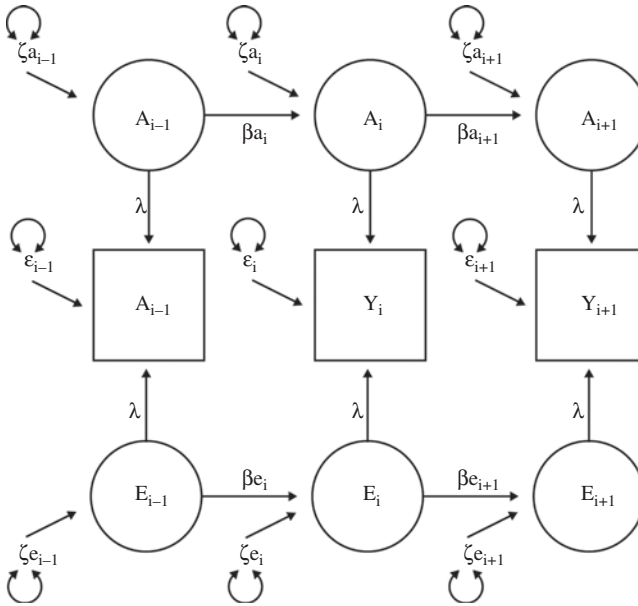

Figure 3.4. A general AE simplex path diagram of arch shape of Australian twins.

approaches. Dizygotic twins are one such group that may be utilized for linkage analysis. Monozygotic twins, on the other hand, are uninformative for linkage unless data are available from other family members. Linkage can localize complex trait loci with 1- to 10-Mbp resolution; however, the locus effect size needs to be more than 10 percent of the trait genetic variance to be detectable. Quantitative trait loci (QTLs) detected by linkage can be considered the hubs of a complex system because of their large influence on trait variation. Because of the natural randomization induced by segregation during meiosis, linkage is robust to confounding. Figure 3.5 illustrates a path diagram incorporating a putative QTL. The intrapair QTL correlation ($\hat{\pi}$) is an estimate (not all relationships are fully informative) of allele sharing identical by descent between DZ twins (Martin et al. 1997). Linkage can be tested by dropping Q from the model and examining the change in model fit; a significant decrease in model fit is suggestive of linkage.

Association (candidate-gene) analysis extracts information from the co-occurrence of traits and markers within individuals. These approaches have traditionally utilized unrelated case/control (or similar) population samples. A key liability with this type of cohort is that underlying population stratification may result in spurious association. Familial structures (and particularly twins), while generally more expensive to genotype, allow for family-based

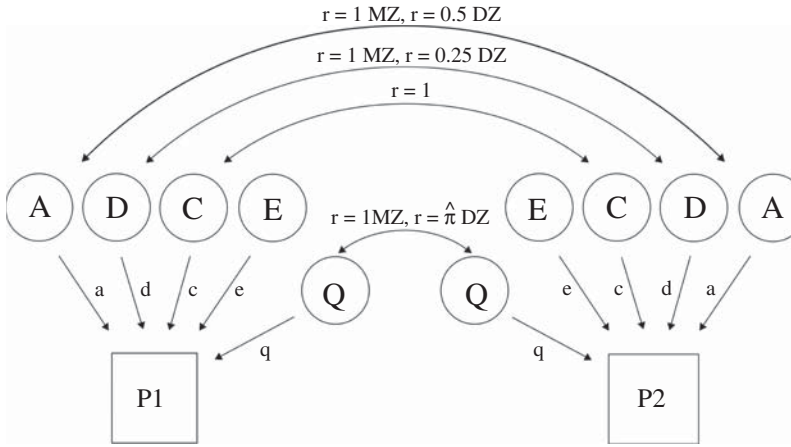

Figure 3.5. A univariate path diagram of the twin relationship, incorporating a genetic marker at a specific locus in order to test for linkage.

approaches (within/between transmission disequilibrium testing) that are robust to the presence of population stratification. Localization of complex trait loci using whole-genome approaches is usually at the 0.01- to 0.1-Mbp resolution, provided the locus effect size is more than 1 percent of the genetic variance. Such loci can be considered nodes within the complex system framework. Association analysis is less robust than linkage analysis.

The flexibility of the SEM approach allows both linkage and association to be modeled simultaneously in familial data sets. Figure 3.6 illustrates a combined model of linkage and association for a phenotype for which molecular marker data are available for sib pairs, and which allows for possible population stratification. Latent variables for family resemblance F, QTL variance Q, and individual-specific variance E cause the phenotypes of two siblings, P1 and P2. S represents half the sum of the sibling pair's genotypic effects, and D represents half their difference. These components contribute to between (B) and within pair effects (W) via parameters b and w, respectively. In the absence of stratification, b and w are expected to be equal. Genuine association with observed genotypes G1 and G2 decreases the size of the linkage-based QTL effect, q.

Using appropriate model specification, SEM can be extrapolated to modern whole-genome approaches, which, in the case of association, can identify causal variants (Vieira et al. 2008). As such, the dental anthropologist can capitalize on comprehensive marker data arising from high-throughput, chip-based approaches to ascertain large numbers of markers simultaneously. There is, however, a concomitant increase in the numbers of statistical tests required, necessitating consideration of the experiment-wise error rate. MERLIN (Abecasis et al.

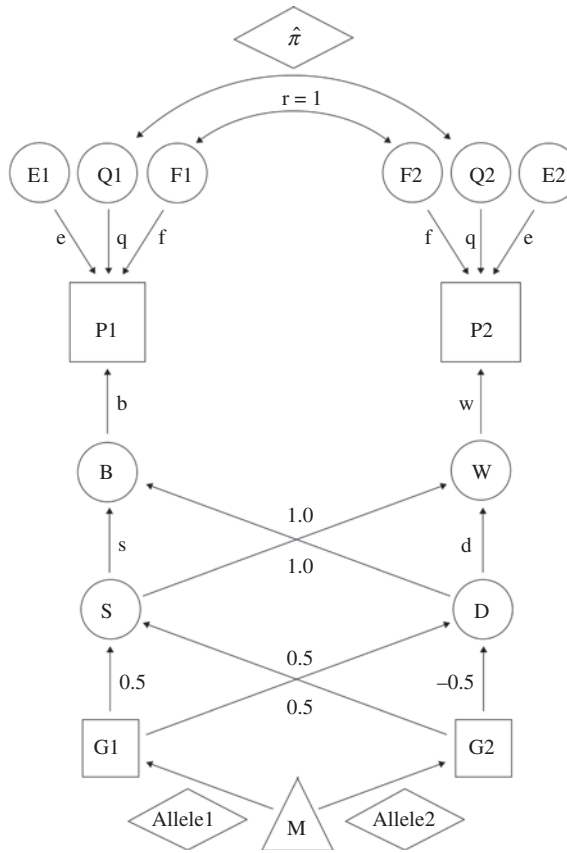

Figure 3.6. A univariate path diagram of the twin relationship incorporating genetic marker information for simultaneous linkage and association analysis, and accounting for population stratification.

2002), a multipoint engine for rapid likelihood inference, is a purpose-built piece of software whose capabilities include linkage analysis (variance components, nonparametric linkage, parametric linkage, clustered marker data), association, haplotyping, information content, error detection (most single-nucleotide polymorphismtyping errors are Mendelian consistent), and simulation.

3.14 Advantages and disadvantages

The classic twin model has several distinct advantages over other familial structures. First and foremost, having access to both MZ and DZ pairs

allows one explicitly to estimate the additive genetic variance without making assumptions regarding the presence/absence/structure of common or "familial" environment effects on trait(s) under study. Further, twins are matched for age, making estimation of common environmental variance, if present, straightforward. Having an "internal" control within twin pairs provides this data structure with a significant advantage for genetic association studies over other population-based cohorts; it is immune to issues of population admixture/structure, because of the ability to develop estimates of gene action using within and between pair approaches. Recent advances in the use of molecular marker data to infer population structure make this less of an issue.

Disadvantages include greater challenges associated with collecting twin data, although this is generally substantially outweighed by the issues outlined previously. For genomic approaches, however, power can be problematic, except where large twin samples are available (e.g., Nordic twin registries). The classic twin model assumes equal variances between zygosity groups, an issue that is normally examined empirically in the raw data. Debate still centers on the common environments assumption of the model, which implies similarly shared environments between twins from different zygosity groups. For behavioral traits influenced by interactions between twins and/or other family members, this is an acknowledged shortcoming. For morphological features measured on the dental crown, issues arising from variation in placentation may be of greater significance; indeed, MZ twins are more likely to share prenatal environment unequally relative to their DZ counterparts. Judicious use of data available on twin chorionicity may go some way toward addressing this issue. Finally, there is the issue of the twin condition itself playing a role in phenotype data, when attempts are made to extrapolate to the nontwin population. Twins generally have shorter gestation lengths and smaller birth weights than singletons. Our own data demonstrated a number of timing differences between twins and singletons in tooth emergence, normally associated with differences in gestation length. If timing is appropriately adjusted for in the model, subsequent findings may be usefully extrapolated to the singleton population.

3.15 Special twin features

Twinning has been associated with a high perinatal mortality rate (Zahalkova 1978) and MZ twins display a higher prevalence of congenital abnormalities; the latter are often related to failure of bilateral structures to fuse properly during development (Boklage 1987). Apart from an apparently higher prevalence of perinatal mortality and morbidity, there is another special feature that

has frequently been overlooked: MZ twin pairs often share a common placenta and chorion (around 60–70 percent). Still, around 20–30 percent of MZ co-twins have separate placentas and chorions. The latter twins are thought to have separated at an early stage of development, probably in the first 5 days post conception; monochorionic twins are thought to have separated around 6 to 9 days post conception. In around 30 percent of monochorionic MZ twins, there can be arteriovenous anastomoses that can lead to marked differences in physical development. Few studies of dental features have taken chorion type into account, although Burris and Harris (2002, 2003) provide evidence that the type can affect permanent tooth dimensions. These researchers suggest that previous estimates of heritabilities for dental traits, where these types of effects have not been considered, are likely to have been biased. Recently, our group found that intrapair variances for tooth-size data in monochorionic Australian twin pairs generally exceeded those for dichorionic pairs; the indication is that the prenatal environment may have an effect on their developing dentitions (Race et al. 2006).

The phenomenon of mirror imaging, where one member of a twin pair "mirrors" the other for one or more features, is well-known. However, most studies have been retrospective reports based on small samples. To ensure that findings are not purely due to chance, a suite of study variables should be defined, measurements and observations made, error studies performed, and comparisons of the frequencies of mirrored features made between MZ twins, DZ twins, and singletons. Given that some preliminary evidence suggests mirror imaging may be related to timing of the division and therefore type of placentation (Townsend et al. 1992), information on chorion type of MZ twins would also be valuable in future studies of mirror imaging.

3.16 The MZ co-twin design

With the completion of the Human Genome Project (Collins et al. 2003), the generation of progressive iterations of the Human HapMap (International HapMap Consortium 2005), and the rapid publication of many large-scale, high-powered whole-genome association studies of human phenotypes, focus has shifted from variation in the genetic code per se to how gene expression is modulated. There is a growing appreciation that epigenetic factors have a major influence on trait expression, and these factors have been implicated in changes over life course (Poulsen 2007). In its broadest sense, epigenetics refers to differential modification of gene effects due to stochastic variation in the local genetic milieu. A more narrow interpretation is the influence of (potentially heritable) changes in local chemical mediators of gene transcription or translation

(CpG methylation, histone deacetylation, X inactivation, etc.). Monozygotic twins provide an ideal model for studying the role of epigenetic factors in trait variance, and there are numerous publications that have provided evidence of epigenetic discordance between MZ twins.

3.17 The opposite-sex DZ design

This approach focuses on male/female twin pairs and tests whether there are differences in mean values and variances for selected features between twins compared with other twin types and singletons. Since each member of a male/female twin pair may be exposed to elevated levels of hormones from the co-twin in utero, it is possible this may lead to observable effects postnatally. Indeed, there is evidence that tooth size is increased in females belonging to opposite-sexed twin pairs (Dempsey et al. 1999; Ribeiro et al. 2012). It remains to be seen whether these apparent effects are related to male hormones on the female in utero, although other species provide some supportive evidence (Fels and Bosch 1971).

3.18 Dental crown data from studies of twins and families – the Adelaide experience

Research relating to human growth and dental anthropology in the University of Adelaide's Dental School dates back to the early twentieth century when Draper Campbell (1925) published his landmark thesis *Dentition and palate of the Australian Aboriginal*. Subsequently, Murray Barrett and Tasman Brown carried out a longitudinal growth study of Aboriginal Australians at Yuendumu in the Northern Territory (Brown et al. 2011). More than 1,700 dental casts of approximately 450 subjects were obtained; these records have enabled detailed analyses of dental development, including studies of tooth emergence and formation of dental arches (Brown and Townsend 2001). Compilation of genealogical records for this population also enabled genetic analyses to be performed with reference to tooth size (Townsend and Brown 1978; Townsend 1980). These studies confirmed a strong genetic influence on variation of dental crown size but also showed that environmental factors played a role.

In the 1980s, a study commenced of the teeth and faces of teenage twins in Adelaide. The main aim was to quantify relative contributions of genetic and environmental influences to variation in dental and facial features. Many papers were published based on data generated from investigations involving

this first cohort of twins; some are detailed in the following. Records collected for this cohort (Cohort 1) included the following:

- oral examinations of all participants to record teeth present and to detect any evidence of dental caries or other problems;
- alginate impressions of the upper and lower dental arches that were cast in good quality dental stone;
- intraoral and extraoral photographs, together with standardized photographs of faces;
- palmprints and fingerprints, as well as information about laterality including hand, foot, and eye dominance;
- detailed medical histories of the twins;
- height and weight measurements;
- blood samples for DNA extraction, zygosity determination and future linkage, association and epigenetic studies.

The study was expanded in the 1990s to include collaboration with Professor Louise Brearley Messer at the University of Melbourne. A second cohort of twins with primary teeth was recruited to allow genetic analyses focusing on dental and facial growth and development. This longitudinal study aimed to collect records at three key times: at the stage when all primary teeth were present (around 3–5 years), when children had mixed dentitions (around 8–10 years), and when all permanent teeth were present except third molars (around 12–14 years). Collection of most records was completed by the mid-2000s, and numerous papers have been published. There is still a significant amount of data extraction and analysis being performed on this cohort, including some with collaborators from Japan and the United States (Richards et al. 1997; Corruccini et al. 2005). Serial records collected (Cohort 2) were similar to those obtained at a single age in Cohort 1, with the exception of the collection of exfoliated primary teeth from each twin.

Most recently, a third cohort has been recruited for a study of tooth emergence and oral health. This study involves an Australia-wide recruitment approach with key collaborations between investigators in Adelaide (led by Professor Townsend), Queensland (Professor Seow), and Western Australia (Professor Gotjamanos). The project is focused on clarifying the extent to which genetic factors contribute to variation in the timing and sequence of emergence of primary teeth. Records currently being collected from Cohort 3 include:

- primary tooth emergence and exfoliation data;
- exfoliated primary tooth crowns;
- oral microbiological data;

- buccal swabs for DNA extraction, zygosity determination and future linkage, association studies and epigenetic studies;
- detailed questionnaires on medical histories of mothers and twins, oral health histories, feeding habits, and so forth; and
- clinical examinations of selected individuals.

There are now more than 1,200 twin pairs enrolled in our investigations, together with some 4,000 relatives. Our broad aim has been to improve understanding of how genetic and environmental factors contribute to variation in dental and facial features, and oral health. We have also used our data to investigate the determination of laterality, particularly mirror imaging. We plan to maximize use of the longitudinal data and DNA collected and continue to collect phenotypes; the purpose is to perform genomewide scans for putative genetic linkage peaks for a range of dental features, and then to test for association between a series of likely candidate genes and our phenotypes. We are also examining trait discordance in MZ pairs for evidence of epigenetic effects.

Our investigations have the approval of the Committee on the Ethics of Human Experimentation, the University of Adelaide (Approval Nos. H-07–84A, and H-78–2003), and all participants are informed volunteers. We have worked closely with the Australian Twin Registry and Australian Multiple Births Association to recruit twins. We have also actively recruited twin pairs for Cohort 3 from newspaper birth announcements, hospitals, and prenatal exercise classes. Retention rates throughout the studies have been high with less than 10 percent attrition.

Zygosities of twins examined in the 1980s were confirmed by comparisons of blood markers (ABO, Rh, Fy, Jk, MNS) together with serum enzyme and protein polymorphisms. Zygosities of twins in Cohort 2 were confirmed by analysis of up to six highly variable genetic loci (*FES*, *vWA31*, *F13A1*, *THO1*, *D21S11*, *FGA*) on six different chromosomes, using DNA from buccal cells. Determination of zygosity for twins in Cohort 3 is being done using nine highly variable genetic loci on nine different chromosomes.

Our group has used a range of approaches to describe dental crown variation in Caucasian twins and other groups over the past 25 years. Many linear dimensions have been acquired directly using calipers, or indirectly using standardized 2-D digital images. More recently, we have been using a 3-D laser surface scanner to construct point-cloud data sets of dental models to obtain more sophisticated morphological measures, including surface distances, areas, and volumes. The scanner is illustrated in Figure 3.7. We have also been using micro computed tomography (micro-CT) to obtain data on internal tooth structure in exfoliated primary crowns from twin cohorts.

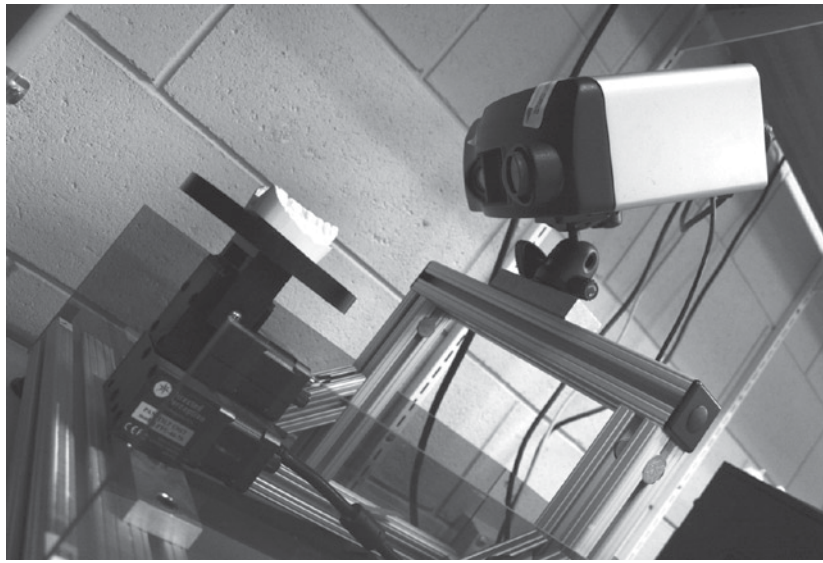

Figure 3.7. A 3D scanner used to acquire point-cloud data from dental casts at the University of Adelaide.

Many different variables have been analyzed, including dental crown size, intercuspal distances, dental arch size and shape, occlusal variables such as overbite and overjet, and various facial dimensions. We reported results of replicability studies showing that errors of the methods are small and unlikely to bias results (Eguchi et al. 2004; Townsend et al. 2003). We have used the generalized structural equation modeling program Mx by Neale et al. (2003) to carry out genetic analyses of dental data. Heritability estimates (h^2), calculated as the ratio of additive genetic variation to total phenotypic variation, have been calculated for several dental phenotypes (Hughes et al. 2000, 2001a, 2001b).

Dental and facial traits have been chosen to represent increasing levels of complexity within the dentition. We have considered factors influencing variation in individual teeth, including intercuspal distances and crown features such as Carabelli trait (Townsend et al. 2003; Townsend and Martin 1992). We have also explored how genetic and environmental factors influence variation in positioning of teeth within and between the dental arches, as well as in selected facial features (Townsend et al. 2006).

Apart from the traditional twin approach, we have used the MZ co-twin design to investigate genetic and environmental influences on dental traits; in this case, one twin shows a feature and the other has a different expression or

does not display the trait (Townsend et al. 2005). We also looked at tooth size in opposite-sexed DZ twin pairs to determine whether there is any evidence for a hormonal influence on dental development in utero (Dempsey et al. 1999a; Ribeiro et al. 2012). Although we have information on chorion type for only a small proportion of our twin samples, we have been able to conduct preliminary investigations of the relationships among chorion type, birth weight, and tooth size (Race et al. 2006).

Teeth, faces, and fingerprints are particularly suitable for studies of symmetry and asymmetry, and we have been interested in studying mirror imaging (Brown et al. 1992; Townsend et al. 1986, 1992).

3.19 A selection of results

Some key findings are summarized in Table 3.1. Models incorporating additive genetic variance (A) and unique environment variance (E) provide the best fits for most dental traits studied to date; however, models including only environmental variance, either unique environment (E) alone or a combination of common and unique environment (C and E), provide the best fits for some molar intercuspal distances. Furthermore, models incorporating common and unique environmental effects (C and E), in addition to an additive genetic effect (A), provide the best fits to explain variation observed in molar crown diameters. Heritability estimates for variables displaying significant additive genetic variance differ considerably, that is, from 28 percent for incisal overjet to 94 percent for primary tooth emergence timing. Intercuspal distances have relatively high phenotypic variation but low to moderate heritabilities. In contrast, crown diameters have relatively low phenotypic variation but moderate to high heritabilities (Townsend et al. 2006).

3.19.1 Permanent crown size

Our group has published a number of estimates of dental crown size variability. Dempsey and Townsend (2001) detailed mesiodistal (MD) and buccolingual (BL) permanent crown dimensions from Cohorts 1 and 2. Univariate biometrical models were fitted to the data, and all variables showed significant contributions of additive genetic variation, from 56 to 92 percent of phenotypic variation, with most above 80 percent.

A significant effect of environment shared by twins prenatally or in early childhood was found for MD and BL diameters of UM1 (22–27 percent). There were also significant levels of nonadditive genetic variation in MD diameters

Table 3.1. *Contribution of genetic and environmental components to variation in selected dental features in Australian twins*

Dental trait	Best-fitting model	h^2	95% CI
Tooth emergence (i_1)	AE	94	91–96
Intercuspal distances (M^1)			
MB–DB	AE	60	29–78
DB–DL	AE	65	49–77
DL–ML	E	–	–
ML–MB	CE	–	–
Crown diameters (I^1)			
MD	AE	88	–
LL	AE	80	–
Crown diameters (C)			
MD	ADE	86	–
LL	AE	85	–
Crown diameters (M^1)			
MD	ACE	59	46–69
BL	ACE	61	51–71
Carabelli trait (M^1)	AE	90	–
Carabelli trait (dm_2)	AE (multivariate)	74	66–81
Carabelli trait (M^1)	AE (multivariate)	81	79–87
Hypocone			
Right M^1	AE	87	65–96
Right M^2	AE	90	80–95
Permanent arch dimensions			
Breadth	AE	82	61–91
Depth	AE	92	81–97
Maxillary arch shape			
Primary	AE (multivariate)	70–79	–
Mixed	AE (multivariate)	67–77	–
Permanent	AE (multivariate)	84–85	–
Occlusal traits			
Overbite	AE	53	28–71
Overjet	AE	28	2–50

of canines and first premolars, which is consistent with selective pressures on these teeth in human evolution.

There was significant sexual dimorphism for tooth crown size, since the mean twin sizes could be constrained to be equal across zygosities within each sex, but not across sexes. This dimorphism did not extend to covariance structure, except for BL breadths of the left UI1 and right UC, which required heterogeneous models for the sexes.

Our results provide no evidence of systematic differences in heritabilities for crown size between teeth within each tooth class, as expected under Butler's

(1939) morphogenetic field concept, or between different crown dimensions of permanent teeth.

Data from opposite-sexed (OS) DZ twin pairs indicate that tooth size of females from OS DZ pairs tends to be larger than those of females from same-sexed DZ pairs or MZ females (Dempsey et al. 1999). This finding provides support for the concept that diffusion of sex hormones from male to female in utero accounts for the increased tooth size. This possibility has been substantiated by more recent work (Ribeiro et al. 2012).

3.19.2 Primary crown size

Maximum mesiodistal and buccolingual dimensions of maxillary and mandibular teeth were measured in Cohort 2 (Hughes et al. 2000). Data were subjected to univariate genetic analysis. A model incorporating additive genetic (A) and unique environmental (E) variation was the most parsimonious for all variables. Heritability estimates for crown size ranged from 62 percent to 91 percent. These data showed that variation has a strong genetic component, similar to that observed in the permanent dentition. Further studies are required to determine whether the underlying genetic mechanisms are the same for deciduous and permanent teeth.

3.19.3 Intercuspal distances

Molecular studies indicate that epigenetic events are important in determining how the internal enamel epithelium folds during odontogenesis. Since this folding leads to the subsequent arrangement of cusps on molar teeth, intercuspal distances of human molar teeth should display greater phenotypic variation but lower heritabilities than overall crown diameters. This pattern was substantiated in a publication (Townsend et al. 2003) that examined intercuspal distances and maximum crown diameters from Cohort 1. Intercuspal distances displayed less sexual dimorphism in mean values but greater relative variability and fluctuating asymmetry than overall crown measures. Correlations between intercuspal distances and overall crown measures were low. Models incorporating only environmental effects accounted for observed variation in several intercuspal measures, and for those intercuspal variables displaying significant additive genetic variance, estimates of heritability ranged from 43 to 79 percent. Those for overall crown size were higher, ranging from 60 to 82 percent. Our finding of high phenotypic variation in intercuspal distances with moderate genetic contribution is consistent with substantial epigenetic influences on the

progressive folding of internal enamel epithelium, following formation of the primary and secondary enamel knots.

3.19.4 Agenesis/supernumeraries

Tooth number is highly conserved in most dentate species; however, there remains significant variation in tooth number in humans. With regard to missing teeth, expression may range from absence of a single tooth to anodontia; there are often concomitant changes in the form of the teeth that are present. Extra or "supernumerary" teeth, while less common, are also found in all human populations. There is growing evidence that the number of teeth is associated with a threshold effect of tooth size, in which individuals with smaller teeth show greater frequencies of mild agenesis and/or peg-shaped teeth; conversely, individuals with larger teeth are more likely to have one or more supernumerary teeth (Brook 2009)

Several dental features, including missing or supernumerary teeth, are expressed differently in MZ twin pairs. Our survey (Townsend et al. 2005) of the prevalence of simple hypodontia and mesiodentes in a sample of nearly 300 MZ pairs yielded frequencies of 9 percent for missing UI2s or UP2s and 3 percent for mesiodentes. These values are similar to those in other twin studies (Markovic 1982; Kotsomitis et al. 1996) but higher than expected in singletons (Graber 1978), indicating we need to remain aware that the special nature of twinning may influence dental development. We noted evidence of at least one missing UI2 or UP2 in 24 of 278 pairs of MZ twins, with 21 pairs showing discordant expression. We postulated that minor variations in epigenetic events during odontogenesis may account for these differences. We are currently undertaking methylation profiling of these discordant MZ pairs and a matched set of controls to determine whether qualitative or quantitative differences in methylation status may play a role in differential trait expression.

3.19.5 Carabelli trait

Expression of this upper molar trait ranges from pits and grooves to protuberances and free cusps. An early publication (Townsend and Martin 1992) aimed to clarify genetic and environmental contributions to trait variation on UM1s in Cohort 1. Estimates of polychoric correlations were obtained between pairs of monozygous (MZ) and dizygous (DZ) twins and various gene-environment models were fitted by a weighted least-squares approach. The favored model included additive genetic effects together with a general environmental

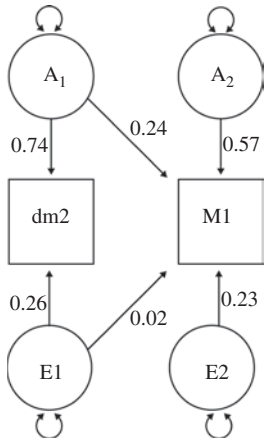

Figure 3.8. A general AE Cholesky decomposition path diagram for Carabelli trait expressed on the deciduous second molars and permanent first molars of Australian twins.

component and an environmental effect specific to each side. An estimate of heritability around 90 percent indicated a very strong genetic contribution to observed variation. The pattern of correlations for MZ and DZ data suggested that further studies involving other types of relatives would be worthwhile for detection of possible nonadditive genetic effects of dominance or epistasis.

More recently, a multivariate structural model containing specific and general additive genetic effects and unique environmental effects was found to be sufficient to describe phenotypic covariation between ages (Hughes and Townsend 2011). Figure 3.8 illustrates the most parsimonious Cholesky decomposition of the observed covariance. Heritability estimates were 74 percent in the udm2 and 81 percent in the UM1. Genetic correlation between the two traits was 0.42, indicating a moderate degree of independence in genes mediating trait expression in the two dentitions. According to Butler's field model, the most mesial tooth within each "field" shows most stability in size and morphology. It has been proposed that dm2 should be considered part of the permanent molar series, based upon ontogeny and phylogeny. This statement is supported by our data; there was a significant transmission of genetic variance from udm2 to UM1.

3.19.6 Cusps 5, 6, and 7

Recently, we presented data on the relative contribution of the genotype to expression of cusps 5, 6, and 7, as well as groove patterning, in primary and

permanent mandibular molars (udm2, UM1, and UM2) from twins in Cohort 2 (Hughes et al. 2010). Arizona State University Dental Anthropology System ASU plaques were used to score phenotypes from dental models. No variation was observed for cusp 5 on ldm2 (complete presence). A model containing additive genetic effects and unique environment effects was appropriate for groove pattern (ldm2, LM1), cusp 5 (LM1), cusp 6 (ldm2), and cusp 7 (ldm2, LM1, LM2). Heritability estimates ranged from 77 to 99 percent. A model incorporating only environmental variation was appropriate for groove pattern (LM2) and cusp 6 (LM1). There was evidence of a shared (twin) environment effect on cusp 5 (LM2) and cusp 6 (LM2).

These data support the role of dm2 as the key tooth of the morphogenetic molar field; the ldm2 was the only tooth for which all four phenotypes were influenced principally by the genotype. Our findings should be interpreted cautiously as sample sizes were underpowered to resolve the applied models (especially for LM2). More data are being collected to develop a multivariate genetic model of molar cuspation and patterning.

3.19.7 Hypocone

Our group has published data on the frequency of occurrence and degree of expression of hypocones on UM1s and UM2s in Cohorts 1 and 2 (Higgins et al. 2009). Hypocones were found to be more common and larger on UM1 than UM2, and there was a tendency for them to be larger in males. No significant differences in occurrence or expression were noted between antimeres, with fewer differences observed between UM1 than UM2. The percentage concordance for expression in MZ twin pairs was higher than in DZ pairs, indicating a genetic influence determining the variation in expression, and the most parsimonious univariate model incorporated additive genetic and unique environmental effects. Narrow-sense heritability estimates for both UM1 and UM2 were high, indicating that a large portion of phenotypic variation could be explained by additive genetic effects. The greater range of phenotypic expression shown by UM2 compared with UM1 may reflect a common genetic liability that is modulated by differences in tooth size, location, and/or developmental timing between teeth.

3.19.8 Interdental spacing variables

We quantified the extent of variation in a range of occlusal features, including interdental spacing, incisal overbite and overjet, arch breadth, and arch depth,

in the primary dentition of Cohort 2 (Hughes et al. 2001b). Univariate genetic analyses were carried out on the quantitative data using normal assumptions of the twin model. Genetic modeling indicated that a model incorporating additive genetic (A) and unique environmental variation (E) was the most parsimonious for interdental spacing, overbite, overjet, and arch dimensions. Heritability estimates for interdental spacing ranged from 62 percent to 81 percent. Estimates for overbite and overjet were 53 percent and 28 percent, respectively, and those for arch dimensions ranged from 69 percent to 89 percent.

3.20 Locating genes affecting dental development

Until recently, the analysis of population- or cohort-based molecular marker genetic data involved whole-genome linkage analysis or association analysis of putative candidate loci. Since the application of a genomewide association study (GWAS) by the Wellcome Trust Case Control Consortium (2007), researchers have applied GWAS to many different phenotypes. Pillas et al. (2010) reported findings from a GWAS of the time at which the first primary tooth emerged in the oral cavity and the number of teeth present at 1 year of age in a Finnish birth cohort. The researchers identified several loci associated with the dental phenotypes under investigation, including some genes known to be involved in dental development, for example, *EDA*, *HOXB2*, and *IGF2BP1*. This study built on the findings of earlier studies by our group that showed that there is a strong genetic basis to timing of primary tooth emergence in Australian twins (Bockmann et al. 2010; Hughes et al. 2007).

Another recent study aimed to clarify whether there was an association between a nonsyndromic polymorphism in the ectodysplasin A receptor gene (*EDAR*) and selected metric and nonmetric dental phenotypes in Japanese (Kimura et al. 2009). The researchers found that one particular *EDAR* allele was strongly correlated with the degree of incisor shoveling, explaining approximately 19 percent of the total variance for the trait. Researchers noted that altered expression of *Edar* and *Eda* affects dental morphology in experimental animals (Mustonen et al. 2003; Tucker et al. 2004), but these effects are not the same as those in humans. This finding emphasizes the need for caution when comparing genetic studies of dental morphology between experimental animals and humans.

3.21 Genetic variance and heritability – a cautionary tale

When one is considering the contribution of the genome to overall variation of a trait within a population, it is important to consider context. Traditional

narrow-sense heritability estimates the relative contribution of the additive effects of genes to phenotypic variance within a *population*; it says nothing about the relative role of genes in trait development within any one individual. Furthermore, extrapolation of such estimates to other groups or populations should be done with caution. Heritability can change without any genetic change occurring (e.g., when the environment starts contributing to more variation). Considering that both genes and environment have the potential to influence dental crown size, heritability could increase if genetic variation increases, causing individuals to show more phenotypic variation (e.g., different crown sizes). On the other hand, heritability might also increase if the environmental variation decreases, causing individuals to show less phenotypic variation (e.g., more similar crown sizes). Heritability increases because genetic factors are contributing more variation, or because nongenetic factors are contributing less variation; what matters is the relative contribution. Drawing inferences regarding population differences in heritability necessitates a sound understanding of the role of environment in trait variance within each population under consideration.

The extent of dependence of phenotype on environment can also be a function of the genes involved. Matters of heritability are complicated because genes may canalize a phenotype, making its expression almost inevitable in all occurring environments. Individuals with the same genotype can also exhibit different phenotypes through phenotypic plasticity, which can make heritability difficult to measure. Recent insights in molecular biology have identified changes in transcriptional activity of individual genes associated with environmental changes. However, there are many genes whose transcription is not affected by the environment.

Short-term evolutionary potential depends on additive genetic variance in a population. Heritability is thus a common measure of evolutionary potential. An alternative is to measure evolutionary potential as the expected proportional change under a unit strength of selection. This approach yields the mean-scaled additive variance as a measure of evolvability. Houle (1992) showed that these two ways of scaling additive variance are often inconsistent and can lead to different conclusions regarding which traits are more evolvable. More recently, Hansen et al. (2011) showed that the correlation between heritability and evolvability is essentially zero. The authors argue this is likely due to inherent positive correlations between the additive variance and other components of phenotypic variance. Thus, heritabilities are often unsuitable as measures of evolutionary potential in natural populations. More generally the authors argue that scaling involves nontrivial assumptions, and a lack of awareness of these assumptions constitutes a systemic error in the field of evolutionary biology.

3.22 The future?

To date, our research group has examined a large range of morphological and oral health phenotypes from a series of three Australian twin cohorts, some of which are reported elsewhere in this chapter. We aim to continue intense phenotyping of Cohort 3, while further extracting data from records already available for Cohorts 1 and 2, to explore further common and unique aspects of dental variation. More and more, we are using geometric morphometric analyses to explore crown size and shape independently to extend our work in nonmetric and traditional linear dimensional traits – using MorphoJ (Klingenberg 2011) and more recently the EVAN toolbox (EVAN Society 2012). We are also seeking to derive more meaningful raw measures in the first instance (areas, volumes, surface distances, etc.). One area of particular interest is the use of micro-CT to explore morphological DEJ variation in exfoliated crowns collected from twins in Cohorts 2 and 3. We also have a particular interest in dental asymmetry as a measure of developmental instability. Possible genetic roles in the development of directional asymmetries in crown form are being examined.

Having already reported heritability estimates for a range of phenotypes, we now plan to develop robust multivariate models of orofacial variation that capture the covariation among dental crown characteristics. High density genetic profiling of the three cohorts is under way, supplemented by data from collaborators. We aim to integrate molecular marker data with our models to identify putative QTLs for further fine-mapping and identification of causal variants; the ultimate aim is to develop predictive models of oral phenotypes. Epigenetic profiling of discordant MZ pairs has become a recent focus of our research group, and we are currently investigating the role of differential methylation in tooth number discordance. Finally, we seek to replicate our initial findings in other data sets and undertake meta-analyses of data sets to improve power.

3.23 Summary

Genetic modeling offers a methodologically robust approach for exploring complexities of dental development and evolution, and this approach articulates well with a conception of the dentition as a complex system. It provides a framework within which to locate evidence of gene effects from high-throughput genotyping. It capitalizes on familial structure, for which twins provide distinct advantages analytically.

This chapter has presented a summary of some key findings from our analyses over the past 25 years. As far as we are aware, our collection of dental

and facial records of Australian twins and their families is one of the largest in the world. We extended our initial morphological investigations of the dentition to longitudinal studies of dental development. Our studies are of relevance to more basic biological issues, including determination of body symmetry, as well as in the fields of physical anthropology and forensic odontology.

Our analyses have shown that there is a strong genetic basis to observed variation in many human dental phenotypes, and there is a significant degree of covariation between many dental phenotypes. We now plan to use a combination of genetic association and genetic linkage approaches to identify or corroborate key genes involved in dental development.

In the last decade, many genes have been identified that regulate epithelial-mesenchymal interactions in developing teeth; the application of both genetic modeling methods and molecular approaches is heralding an exciting new era in dental anthropology research. Our focus is to maximize use of longitudinal data and DNA already collected from our cohorts by performing a genome-wide scan to identify association between likely candidate genes and phenotypes of interest.

Acknowledgments

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4 *Teeth, morphogenesis, and levels of variation in the human Carabelli trait*

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4.1 Introduction

If we are what we eat, then no anatomical structure plays a greater role than our teeth in establishing our biological identity. Across mammals, the shape of teeth corresponds closely with diet. The great variety of tooth shapes that have evolved among mammals underscores the underlying plasticity of teeth from a developmental standpoint. For a type of tooth to evolve, it must be possible for that type of tooth to develop. The relative ease with which features of tooth shape are made in development may manifest themselves in the frequency at which such features appear as variations within populations, become fixed within populations, and ultimately evolve. With the rapid rates of evolution observed among mammals, due in no small part to the potential for rapid evolutionary change in teeth, mammals clearly have teeth that are themselves highly evolvable. Exactly why mammalian teeth are so evolvable is wrapped up in how our teeth take shape during development.

In proposing their "Morphodynamic Model" for tooth formation, Salazar-Cuidad and Jernvall (2002) demonstrated how mammalian dental morphology emerges from a dynamic interaction between genes expressed during cusp formation and a tooth's developing size and shape. Their model is predicated on the molecular signaling activity of enamel knots, transient nondividing epithelial cell clusters that mark the sites of future cusp tips. During the cap through early bell stages of tooth formation, enamel knots secrete both activator and inhibitor molecules (Salazar-Cuidad and Jernvall 2002). Activators not only

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promote epithelial folding and growth downward from the presumptive cusp tip, but also stimulate the formation of new enamel knots, and hence new cusps, in a developmental "cascade" (Jernvall and Jung 2000). Inhibitors, in addition to promoting mesenchymal growth, prevent the formation of new enamel knots within a zone of inhibition surrounding each enamel knot (Salazar-Cuidad and Jernvall 2002). Thus, a new enamel knot can only form at a distance from an earlier-formed enamel knot as determined by the rates of diffusion of activators and inhibitors as well as by the volume of tissue into which these molecules diffuse. In this model, variation in the timing of enamel knot initiation, the length of time during which morphogenesis occurs, and the shape of cusps are all hypothesized to affect realized cusp patterns (Jernvall and Jung 2000). By altering model parameters (e.g., relating to diffusion rates and growth rates), Salazar-Cuidad and Jernvall (2002) successfully predicted dental morphologies similar to those present in extant mice and voles.

Until recently, the morphodynamic model has been used to explain cusp number, size, shape, and configuration in mice, voles (Salazar-Cuidad and Jernvall 2002), and ringed seals (Salazar-Cuidad and Jernvall 2010). It has also been used to predict cusp variation in chimpanzees (Skinner et al. 2010). In principle, the model should hold for the teeth of all mammals, including those of humans. Indeed, Jernvall and Jung (2000) suggest that a simple test of the model in humans would involve predicting variation in the presence and size of the Carabelli cusp, an accessory cusp on the mesiolingual slope of the protocone.

The Carabelli trait is routinely used in studies of human population affinities (see Scott and Turner, 1997, for a summary) and has been noted to vary among hominin species (e.g., Guatelli-Steinberg and Irish 2005; Irish and Guatelli-Steinberg 2003; Reid and Van Reenan 1995; Sperber 1974; Wood and Engleman 1988). The trait ranges in expression from a shallow furrow to a cusp with a free apex that can rival the size of the hypocone (Scott and Turner 1997). Given the use of this trait in studies of human biodistance and its possible use in analyzing hominin phylogeny, an understanding of the trait's developmental biology is useful for evaluating both its potential for homoplasy and the degree to which it can be expected to be linked to the presence of other cusps.

Cusps in the same position as the Carabelli trait are not unique to humans and our close relatives. Variously called the "protostyle" (Matthew 1937; Osborn 1907) or the "pericone" (Van Valen 1978), a small cusp mesial and lingual to the molar protocone is a feature of some other extant and extinct mammals. Notably some members of the archaic ungulate family Periptychidae from the Paleocene of North America evolved upper molars with equal sized cuspules in the Carabelli and hypocone positions, flanking the protocone. Although the hypocone has evolved into an enlarged main cusp on the molars of many

mammalian lineages and become incorporated into derived tooth shapes, the same cannot be said of cusps in the Carabelli position. Nevertheless, understanding the factors that promote initiation and elaboration of the Carabelli cusp provides insight into cusp-making in general.

Because the cusp form of the Carabelli trait is present at the enamel-dentine junction in human teeth (Sasaki 1997; Sasaki et al. 1971), the trait is related to the folding of the enamel epithelium. If a Carabelli enamel knot coordinates this folding and forms as part of a cascade of enamel knot activation, then variation in the Carabelli trait should be predictable on the basis of the morphodynamic model. A predictive feature of the model is that the likelihood of forming new enamel knots increases as distances from the inhibition zones of preexisting enamel knots increase. The Carabelli cusp usually begins to form after the principal cusps have initiated (Kraus and Jordan 1965). Therefore, whether a Carabelli enamel knot has the opportunity to form will depend on the spacing of earlier-forming enamel knots in relation to available space and time on the developing crown. These developmental events can be inferred from the spacing of cusp tips, which reflect the former position of enamel knots, and the size of the crown, which reflects the space and time available for enamel knots to form before morphogenesis ceases. Furthermore, teeth with the most closely spaced cusp tips relative to crown size are likely to have allowed more time for Carabelli cusp growth, either through earlier initiation of the Carabelli cusp, an extended period of morphogenesis associated with larger crown size, or both.

Previous research found correlations between Carabelli expression and crown size as well as other factors associated with crown size – findings that are broadly consistent with the morphodynamic model (Harris 2007; Kondo and Townsend 2006). Over the past few years, our research group has investigated specific predictions of the model for Carabelli trait expression (Durner et al. 2011; Hunter et al. 2010; Moormann et al. 2011; Weston et al. 2009). In addition to testing basic predictions of the model for presence and size of the Carabelli cusp (Hunter et al. 2010; Weston et al. 2009), we are interested in knowing at what levels (individuals, sexes, populations) variation in tooth morphogenesis manifests itself in differences in tooth shape. In other words, does tooth shape at different levels of biological organization vary in ways that are predictable from understanding tooth morphogenesis? We therefore have investigated the extent to which the model can account for differences in the expression of Carabelli cusps in left-right antimeres (Hunter et al. 2010) and metameres, or adjacent tooth positions (Moormann 2011), as well as differences in Carabelli expression between the sexes and across populations (Durner 2011). Finally, we examined the extent to which the Carabelli cusp is associated with a range of accessory cusps. The model predicts that they should covary, because, as Jernvall and Jung (2000) explain, any "parameter

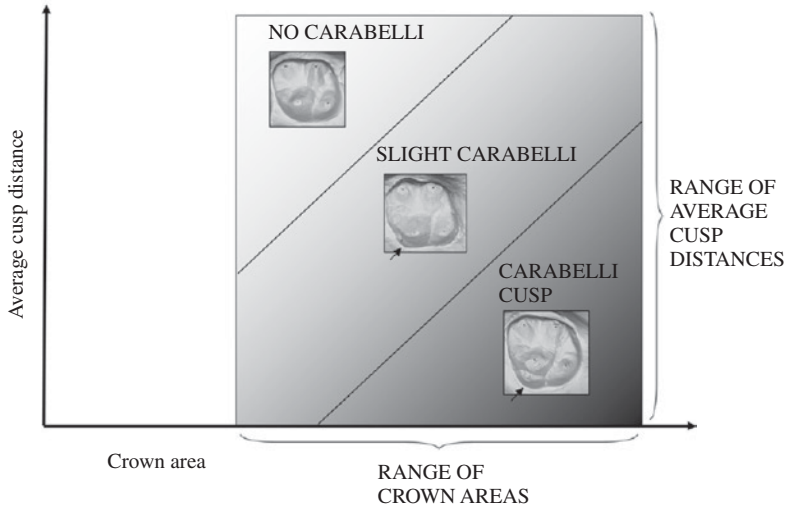


Figure 4.1. Predicted associations between cusp spacing and tooth size with Carabelli trait expression. (Please see color plate section.)

change" in the program of enamel knot activation would affect the entire cusp pattern. Here, we summarize the results of these investigations, which together reveal the ability of the morphodynamic model to explain these multiple facets of Carabelli expression.

4.2 Testing the hypothesis that Carabelli trait expression on UM1s depends on average intercusp spacing relative to crown size

Because spacing of cusp tips in a fully formed crown reflects the spacing of enamel knots during morphogenesis, we predicted that (1) UM1s with smaller average distances among their main four cusps relative to the size of the crown would be more likely to exhibit the Carabelli trait, and (2) UM1s with the smallest relative average intercusp distances would have the most developed Carabelli traits: that is, they would be more likely to form as large cusps (Hunter et al. 2010; Weston et al. 2009). Figure 4.1 graphically summarizes this prediction, in which Carabelli trait expression depends inversely on average intercusp distance, and directly on crown size. Figure 4.2 diagrams an example in which teeth of equivalent size, but with differences in enamel knot spacing, have different Carabelli expression outcomes.

In a dental cast sample of 376 right and left UM1s from an orthodontist in Dayton (see Materials and methods), we found that Carabelli trait expression

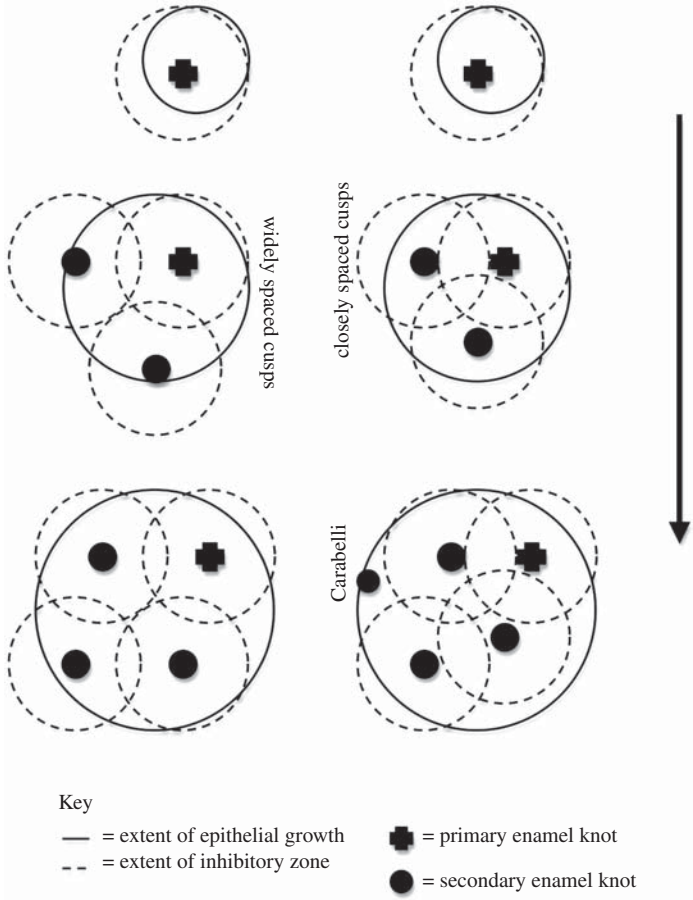


Figure 4.2. Example of patterning cascade model of tooth morphogenesis and Carabelli formation. On two same-sized teeth, Carabelli's cusp is more likely to escape inhibitory signalers and form before cessation of morphogenesis on a tooth with closely spaced cusps. The Carabelli enamel knot is pictured without an inhibitory zone.

meets our predictions. As shown in Figure 4.3, teeth with lower mean intercusp distances relative to tooth size are more likely to have a Carabelli cusp (scored here as "Present"), while teeth with higher intercusp distances relative to tooth size are more likely to lack the cusp ("Absent"). The "Present" and "Absent" data points show minimal overlap on this plot of mean intercusp distance versus square root tooth area. Teeth with slight expressions of the Carabelli trait (i.e., noncuspal forms) overlap the ranges of the other two groups.

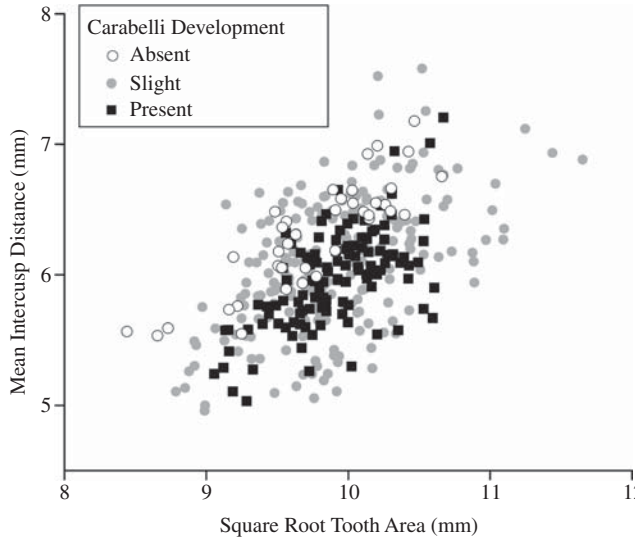


Figure 4.3. Interaction of cusp spacing and tooth size covaries with Carabelli trait expression (Dayton sample).

We performed two primary sets of statistical analyses, in each case for right (n = 187) and left (n = 189) teeth separately. As detailed in the Materials and methods section, percent measurement error ranged from 12 to 32 percent for linear intercusp distances, 10 percent for tooth area, and 4 percent for Carabelli area, with these values being the percentage of total variation in the data set due to repeated measurements within individuals as determined by an ANOVA. Linear intercusp distances were subject to relatively high error as a result of the small distances measured (~2–9 mm) and subjectivity of locating cusp tips. Given this level of error, we expected a fairly high level of noise in the results, which our large sample size helps mitigate. Further increasing the variation in our data set is the likelihood that many developmental factors influence the formation and eventual location of a new cusp – and we are focusing on just one: relative cusp spacing. Therefore, we caution that our analyses were not conducted to determine the predictive ability of any relationships. Instead, we conducted our analyses to detect relationships we expected might be weak a priori, given our level of measurement error within individuals and other potential sources of variation among individuals.

In the first set of statistical analyses, we scored the Carabelli trait using the Arizona State University Dental Anthropology System (ASUDAS; Turner et al. 1991) scoring. ASUDAS score was analyzed as a function of relative intercusp distance, using ordered logistic regression. For both rights and lefts,

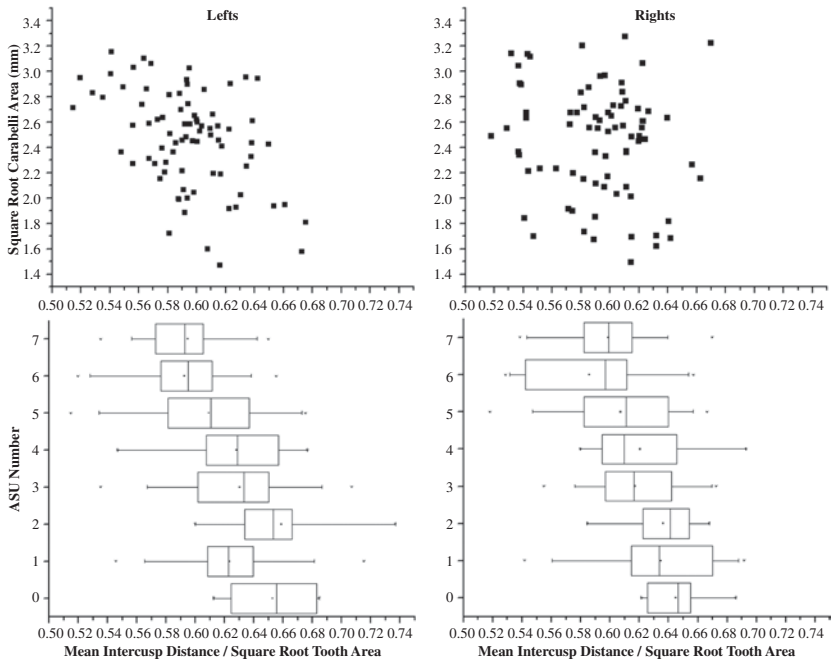
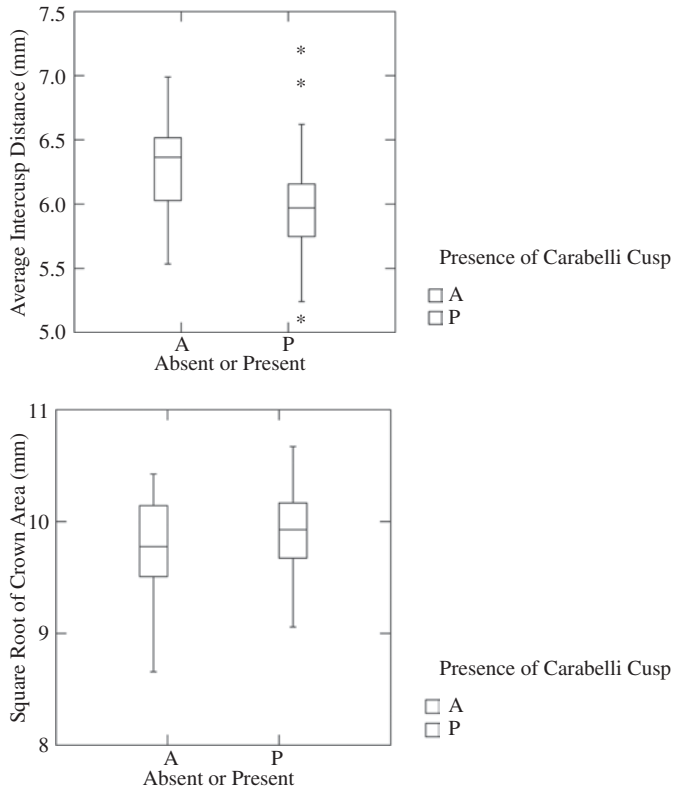


Figure 4.4. Carabelli trait expression and relative cusp spacing across individuals (lefts and rights separate) in the Dayton sample.

there were statistically significant ($p < 0.001$) negative relationships between ASUDAS score and relative intercusp spacing. These relationships are illustrated in the lower two graphs of Figure 4.4. Relative intercusp distances in our sample (ratio of mean intercusp distance to square root of tooth area) range from approximately 0.5 to 0.7. Scaling the logistic regression coefficients by 0.1 (about half of the range of relative intercusp spacing) and exponentiating them revealed that teeth with lesser relative intercusp distances are eight times more likely to have higher ASUDAS Carabelli trait scores than teeth with 0.1 greater relative intercusp distances. In our second set of analyses, using teeth with measurable Carabelli cusp areas (80 lefts and 79 rights), we analyzed whether the size of the Carabelli cusp also depends on relative intercusp spacing. For left UM1s, the square root of Carabelli cusp shows a slight association with relative intercusp distance (Kendall's $\tau = -0.26$, $p < 0.001$, $df = 78$). For rights, the relationship, though near zero and not statistically significant, is negative (Kendall's $\tau = -0.096$, $p = 0.11$, $df = 77$). The upper two graphs in Figure 4.4 illustrate these relationships.

Although the presence of Carabelli cusp might be expected to contribute to crown size, potentially resulting in autocorrelation between the presence of the



Figures 4.5. (A) Box plots for absolute average intercusp distance and (B) the square root of crown area, for left molars in the Dayton sample separated by those with Carabelli cusps (present) and those without (absent).

cusp and size of the crown, we showed that this was not the case in our sample of UM1s. To investigate this possibility, using only one tooth from each antimeric pair (lefts), we compared mean absolute intercusp distance and the square root of tooth area for teeth with and without cusp forms of the Carabelli trait. A two-tailed t-test for the difference between the means of two samples and unequal size and equal variance revealed that teeth with Carabelli cusps have a statistically significantly lower mean absolute intercusp distance than do teeth that lack them (5.98 vs. 6.30 mm, respectively, $t = 3.124$, $p = 0.003$, $df = 74$). The difference in means can be seen in a box plot (Figure 4.5A). However, the mean square root of tooth area is not statistically significantly different between teeth with and without Carabelli cusps (9.91 vs. 9.74 mm, respectively, $t = –1.521$, $p = 0.132$, $df = 74$). The similarity in means and overlap in range can be seen in a second box plot (Figure 4.5B). These findings suggest that differences in

absolute intercusp spacing are driving the relationship between mean relative intercusp distance and Carabelli expression. Although an association between mean absolute intercusp distance and Carabelli expression does not reveal direction of causation, it is likely that Carabelli expression is a consequence rather than a cause of the spacing among the main tooth cusps, which generally initiate earlier than the Carabelli cusp (Kraus and Jordan 1965).

In these analyses, we chose to use mean intercusp distance because, on the basis of the morphodynamic model, the average distance among cusps should reflect the overall "patterning cascade" (Jernvall and Jung 2000) of enamel knot activation. However, we suspected that, given its position, the Carabelli cusp might be particularly sensitive to local developmental events (e.g., rates of inhibitor diffusion) surrounding the protocone. Assuming that the sequence of enamel knot activation is the same as that of cusp initiation (i.e., paracone, protocone, metacone, hypocone; Kraus and Jordan 1965), we further expected that the distance between paracone and protocone would be the most closely associated with Carabelli expression. In fact, Jernvall and Jung (2000) were the first to speculate that Carabelli expression might be a particular consequence of a paracone-protocone-Carabelli cascade of enamel knot formation.

In a follow-up study (Durner 2011), we explored the association of different intercusp distances with Carabelli expression. To do so we used a sample of 197 UM1s from a South Carolina Gullah population and 183 UM1s from Florida Seminoles (see Materials and methods). Holding population, sex, and crown area constant, we conducted partial correlation analyses between ASUDAS Carabelli score and each of the six intercusp distances: paracone-protocone, paracone-metacone, metacone-protocone, paracone-hypocone, protocone-hypocone, and metacone-hypocone.

For 182 right teeth, the ASUDAS score exhibits weak, statistically significant correlations with metacone-protocone distance ($r = –0.19091$, $p < 0.0195$) and paracone-metacone distance ($r = –0.16170$, $p < 0.0306$). The correlation between ASUDAS score and paracone-protocone distance is not statistically significant ($r = –0.13352$, $p < 0.0748$), but is in the expected direction. For 198 left teeth, there are no statistically significant relationships.

These results suggest Carabelli trait formation is more closely related to distances among the paracone, protocone, and metacone. With sex, population, and crown area statistically controlled, the degree of Carabelli trait development increases when the three cusps of the trigon are closer together; the implication is that all of these distances are related as part of an overall cusp-spacing developmental program. The lack of any statistically significant association between the Carabelli trait and distances between the hypocone and each of the trigon cusps may suggest the hypocone is independent of, or is at least freer

to vary from, the trigon patterning cascade. Jernvall (2000) also suggested that trigonid and talonid cascades may be partially independent.

4.3 Antimeric (left and right UM1s) and metameric (UM1s and UM2s) variation in Carabelli expression

Thus far, we have presented evidence demonstrating how the morphodynamic model can account for some variation in Carabelli trait expression among individuals. In this section, we examine the applicability of the model to explain variation in Carabelli expression within individuals. Specifically, we address questions of trait asymmetry in expression in UM1 antimeric pairs and differences in expression between UM1s and UM2s.

Examining asymmetries in Carabelli expression provides an opportunity to test the model's predictions when genotype is held constant. Thus, here we are able to determine whether small right-left differences in enamel knot spacing and/or right-left differences in the duration of morphogenesis arising during development can affect Carabelli expression. Using 89 individuals from the Dayton sample for whom Carabelli cusp area could be measured on the right or left antimere, or both, we tested the hypothesis that individuals with smaller relative intercusp distances on one side would also have larger Carabelli cusps on that side (Hunter et al. 2010). Figure 4.6 shows the relationship between right-left differences in square root Carabelli area and right-left differences in relative intercusp distance. As predicted, the two variables are negatively, though weakly, related (Kendall's $\tau = -0.196$, $p = 0.003$, $df = 87$). When we removed the effect of zeros on the correlation (i.e., where we could measure Carabelli area on right or left teeth, but not both), the negative relationship, while still evident, diminished in strength and significance, though in the predicted direction ($N = 71$ individuals; $Y = 20.0082 - 1.8968X$; Kendall's $\tau = -0.1147$, $p = 0.0793$, $df = 69$).

Carabelli expression is also known to vary across metameres; the trait is far more often expressed and fully developed on UM1s than on UM2s or UM3s (Scott 1979; Scott and Turner 1997). Because UM2s are usually reduced in size relative to UM1s, diminished Carabelli expression would be consistent with the morphodynamic model if mean intercusp distance in UM2s were not reduced in proportion to the reduction in crown size. In other words, we hypothesized that differences in Carabelli trait expression between UM1s and UM2s would be associated with differences between them in average relative intercusp distance, primarily related to smaller UM2 size.

In an expanded sample from the Dayton orthodontic collection used by Hunter et al. (2010), Moormann (2011)) examined the relationships among

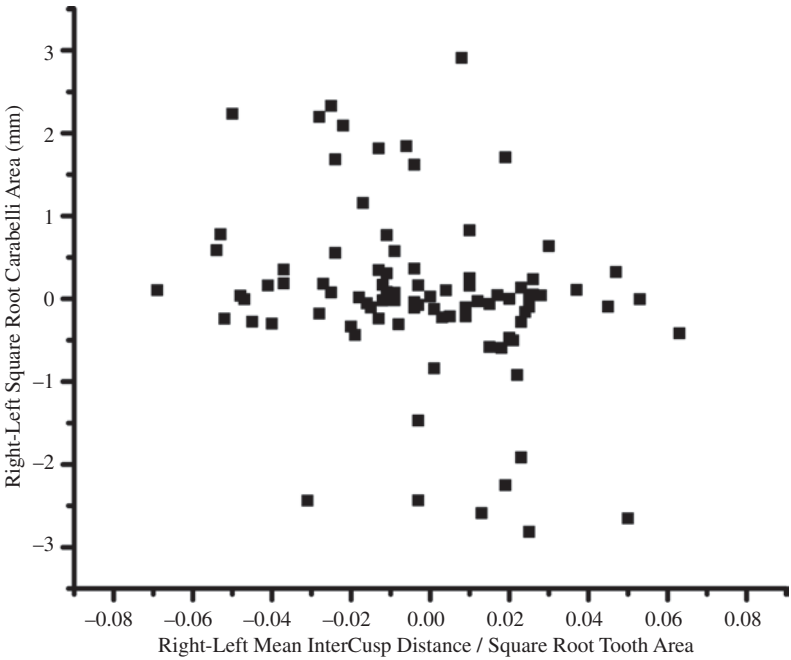


Figure 4.6. Asymmetry within individuals in Carabelli size and relative cusp spacing in the Dayton sample.

Carabelli expression, crown size, and mean intercusp distance in UM1s and UM2s. In the entire sample of UM1s (rights and lefts), 267 of 628, or 43 percent, exhibited ASUDAS grades between 1 and 4; 237, or 38 percent of the sample, expressed a well-developed Carabelli cusp (ASUDAS grades 5–7). Of 366 UM2s, 85, or 23 percent of the sample, had Carabelli traits of grades 1–4; only 19, or 5 percent of the sample, exhibited fully developed cusps (ASUDAS grades 5–7).

We performed paired t-tests on cusp spacing and the square root of crown area on UM1s and UM2s from the same individuals. For right teeth (117 total), the mean difference between the square root of crown area in UM1 and UM2 (0.754 mm) is statistically significant ($t = 15.895$, $df = 116$, $p = 0.000$), with smaller values for UM2. The mean difference between absolute intercusp distance between UM1 and UM2 (0.369 mm) is also significant ($t = 7.382$, $df = 116$, $p = 0.000$), with smaller values for UM2, as would be expected if intercusp distance scales with crown area. However, whereas the percentage decrease in square root crown area from UM1 to UM2 is ~8 percent, that for absolute intercusp distance is ~6 percent. Similar results were obtained for left UM1s and UM2s. Thus, although cusp spacing decreases with crown area,

it does so with negative allometry. We further assessed, again using a paired t-test, whether relative intercusp distance differs between UM1 and UM2. The mean difference in relative intercusp distance is –0.014, which is significant ($t = –2.941$, $df = 116$, $p < 0.004$). Thus, from UM1 to UM2, there is a greater decrease in the square root of crown area than there is in average absolute intercusp distance; the result is greater relative intercusp distances in UM2s than in UM1s. Greater UM2 relative intercusp distance is in turn associated with diminished expression of the Carabelli trait. Conversely, variability in UM1 Carabelli expression appears to be driven by distances among enamel knots – as reflected in absolute intercusp distances rather than by variation in duration of morphogenesis or space associated with crown size.

4.4 Variation in Carabelli trait expression across populations and between sexes

Many previous studies have documented population variation and sex differences in Carabelli trait expression. High prevalence has been noted for European- and African-descended populations (Alvesalo et al. 1975; Hassanali 1982; Mayhall et al. 1982; Meredith and Hixon 1954; Scott 1980; Turner and Hawkey 1998), with lower prevalence noted for Asian-descended populations (Hanihara 1968; Hassanali 1982; Scott 1980; Suzuki and Sakai 1957). Although some studies found no sex difference in expression (Alvesalo et al. 1975; Garn et al. 1966; Harris 2007; Hassanali 1982; Kieser 1978; Saunders and Mayhall 1982; Scott 1980; Thomas et al. 1986; Turner 1969), others found the trait to be sexually dimorphic, generally with males having greater expression (Goose and Lee 1971; Kaul and Prakash 1981; Kondo and Townsend 2006; Tsai et al. 1996; but see Kieser and Preston, 1981, for a case in which females have greater expression).

We hypothesized that developmental events resulting in variation of cusp spacing relative to overall crown size underlie observed differences in Carabelli expression among populations and between sexes. Specifically, we predicted that the trait will increase in size and distinctiveness as intercusp spacing, relative to tooth area, decreases. We further predicted that population and sex will not have independent effects on expression. Townsend et al. (2003) found a smaller degree of sexual dimorphism in intercusp spacing than in buccolingual or mesiodistal diameters, again suggesting that intercusp distances do not scale isometrically with crown area. Given their finding, we expected that with smaller relative intercusp spacing than females, males would be more likely to exhibit the Carabelli trait. In short, we predicted that when relative intercusp spacing is statistically controlled, there

would be minimal or no residual variation in trait expression associated with population or sex.

To test this prediction, we used a sample of 197 UM1s from the aforementioned Gullah, and 183 UM1s from the Seminole. For the combined sample of right and left teeth, Durner (2011) found that the Gullah, in line with previously noted population patterns, exhibited greater Carabelli development than did the Seminole; however, much of the difference appeared to be due to greater development in the male Gullah. Here, we performed a general linear model (GLM) regression analysis on 30 right and 32 left teeth with measurable Carabelli areas. The square root of area is the criterion variable, and the predictor variables are sex, population, the interaction of sex and population, and average relative intercusp distance. For right teeth the squared multiple R for the model is 0.612. The analysis of variance reveals no statistically significant effects of sex ($F = 0.088$, $p = 0.769$), population ($F = 0.294$, $p = 0.592$), or their interaction ($F = 1.080$, $p = 0.309$). The model does, however, show highly significant effects of average relative intercusp distance on square root Carabelli area ($F = 33.763$, $p = 0.000$). These tests were replicated on the left teeth with similar outcomes. The least squares means (i.e., estimated means based on adjusting for other factors in the model), for sex and population, are shown in Figure 4.7.

Results suggest that for these two samples, mean relative intercusp distance is the primary determinant of Carabelli size, regardless of sex or ancestry. It is

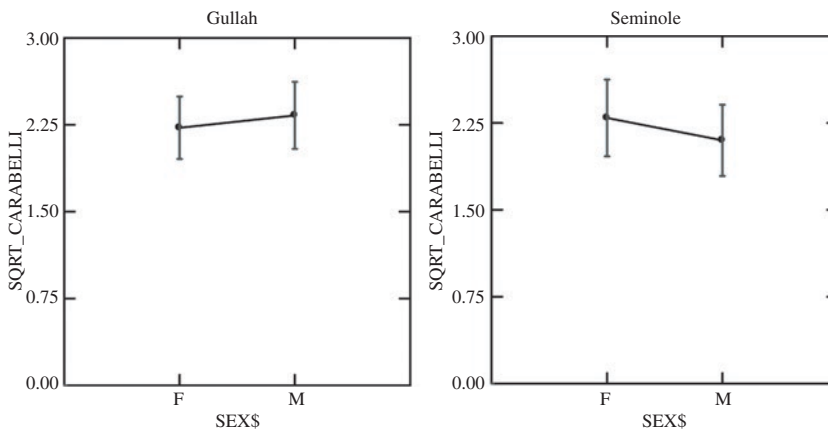


Figure 4.7. Least squares means and standard error bars by population (Gullah, Seminole) and sex from the general linear model (GLM). These are the means for the sexes of each population sample when adjusted for the significant effect of relative intercusp distance in the model. The y-axis is the square root of Carabelli area (in mm). The x-axis is female (F) versus male (M).

interesting to note that when compared to Gullah females, Seminole males, and Seminole females, the 16 Gullah male teeth with measurable Carabelli cusp areas had the highest mean value for square root Carabelli area (2.447 mm) and the lowest value for mean relative intercusp distance (0.621). These values for Gullah males are consistent with basic patterns in the data from Durner (2011), whereby male Gullah (in the combined sample of right and left teeth) have greater Carabelli development than female Gullah and both sexes of the Seminole.

4.5 Correlations with other accessory cusps

Scott (1979) showed that the presence of the Carabelli trait is associated with that of the hypocone. Moorman (2011) and Moormann et al. (unpublished data) replicated this finding in the Dayton sample of UM1s and UM2s separately. Associations between these traits would be expected on the basis of the mophodynamic model: the same factors affecting presence of the hypocone would be expected to affect presence of the Carabelli trait. Specifically, relative to their size, teeth with smaller intercusp distances among trigon cusps would be more likely to exhibit later developing cusps, such as a small, low hypocone or a Carabelli cusp. Moreover, one would expect that the Carabelli trait would be associated with a range of accessory cusps that would also be more likely to form as mean relative intercusp distance among the tooth's principal cusps decreases.

Moorman (2011) and Moormann et al. (unpublished data) tested the association between Carabelli trait and the mesial accessory tubercle, mesial paracone tubercle, protoconule, metaconule, lingual paracone tubercle, and cusp 5. These cusps were identified on the basis of descriptions by Turner and Scott (1997). In a sample of 312 left and 317 right Dayton UM1s, we performed a proportional logistic regression with ASUDAS Carabelli score as the dependent variable and the number of accessory cusps as the independent variable. For both rights and lefts, there were statistically significant ($p < 0.05$) positive relationships between ASUDAS score and the number of accessory cusps, as measured by a likelihood ratio (G) test. In left UM1s when the number of accessory cusps increases by one, the probability of developing a more fully expressed Carabelli cusp increases by 1.3:1. In right UM1s, the odds ratio is 1.2:1. These relationships can be seen in Figure 4.8 (right and left UM1s combined), which demonstrates that across Carabelli grades 0–6, the number of accessory cusps increases. However, the trend across grades is not continued in teeth with grade 7, which may be a result of the small sample size in this grade.

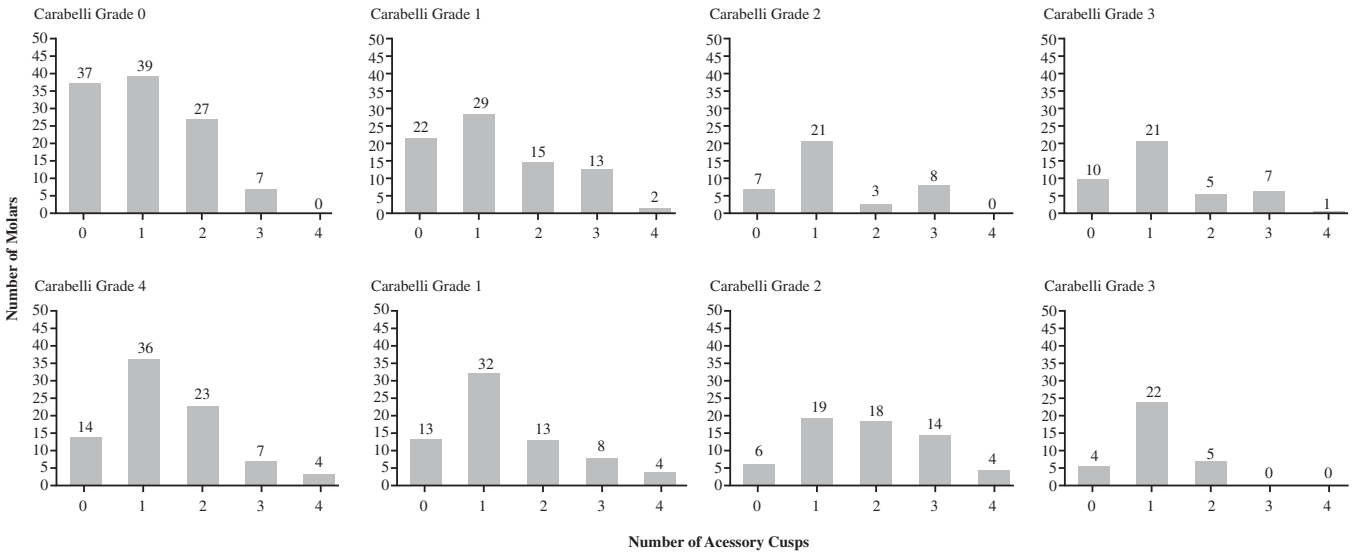


Figure 4.8. Number of accessory cusps versus number of teeth per each Carabelli grade for first molars (right and left combined) in the Dayton sample. Each box represents a different ASUDAS grade. The x-axis represents the number of accessory cusps expressed on each molar. The height of the bar represents the number of molars in each category.

4.6 Discussion and conclusions

In total, our findings demonstrate that at multiple levels of biological organization, Carabelli trait variation is consistent with the morphodynamic model. Our central prediction, based on key components of this model, is that variation in presence and size of the Carabelli trait should be associated with distances among UM1 principal cusps relative to overall crown size. This prediction assumes there is a degree of independence between intercusp distance and crown size. We suggested that these measurable crown features reflect developmental events: distances among cusps tips reflect the former position of enamel knots, while size of the crown reflects the space and time available for enamel knots to form before morphogenesis ceases. In teeth with closely spaced enamel knots relative to available space, a new enamel knot would be more likely to form beyond the inhibition fields surrounding earlier-forming knots. Furthermore, in teeth with the most closely spaced enamel knots relative to tooth size, the Carabelli cusp would grow to larger size, as such close relative spacing would imply: (1) earlier initiation of the Carabelli cusp, (2) an extended period of morphogenesis associated with larger tooth size, or (3) both.

Previous researchers have noted broad consistency between Carabelli trait variation, or other aspects of human cuspal variation, and the morphodynamic model. Kondo and Townsend (2006) and Harris (2007) found significant associations between various measures of tooth size (including absolute intercusp distances) and Carabelli expression. Other factors being equal, the extended time and space associated with larger crowns would promote formation of accessory cusp enamel knots. In addition, Townsend et al. (2003) found that distances between principal cusps had larger coefficients of variation and fluctuating asymmetry scores than did measurements of overall crown size. As the authors note, their result is consistent with experimental work suggesting distances between enamel knots, and hence cusp tips, are not under direct genetic control but are the result of ‘‘a cascade of epigenetic events’’ (Townsend et al. 2003:355).

Our research takes such noted consistencies with the model one step further, providing a rigorous test of specific conditions under which new enamel knots will form under the model’s assumptions. Thus, we find, as specifically predicted by the model, that it is not crown size per se, but spacing of cusps relative to crown size that is most clearly associated with the presence and size of Carabelli trait in most comparisons. Our asymmetry findings are analogous to those of Townsend et al. (2003), indicating that genotype alone does not determine cusp pattern. Because cusps form as a consequence of developmental events, they are subject to developmental noise. Our results suggest that

developmental noise resulting in variation in cusp spacing and/or crown size within an individual results in bilateral asymmetries in Carabelli trait expression that are predictable on the basis of the morphodynamic model.

One of the strengths of our approach is sample size. The large number of dental casts available for measurement made it possible to detect patterns in the data that may not have reached statistical significance in smaller samples, given the measurement error associated with some measurements (see Materials and methods). However, we are unable to account for why some relationships were significant for right teeth but not for left or vice versa. We suggest that measurement error, developmental noise, or both may be responsible.

In this chapter, we also investigated several other aspects of Carabelli expression that we found to be predicted consequences of the model. Differences in Carabelli expression between metameres appear to be associated with the fact that from UM1 to UM2, crown size decreases to a greater extent than does average intercusp distance. With larger relative intercusp distances, UM2s are less likely to exhibit the Carabelli trait, including cuspal forms. Differences between sexes and two samples were also found to be largely explained by differences in relative intercusp distance. However, differences between sexes in relative cusp spacing appear to result more from tooth size differences than differences in absolute cusp spacing (Townsend et al. 2003). Finally, it is not just the Carabelli trait that is associated with relative intercusp distance, but also the hypocone (Moormann 2011; Moormann et al. unpublished data; Scott 1979) and several additional accessory cusps. It is interesting that the Carabelli trait has also been found to be positively associated with the protostylid (Scott 1978), an accessory lower molar cusp. This correlation, which is all the more remarkable since the Carabelli cusp and protostylid are not functionally related, suggests the existence of individual level influences on enamel knot spacing and/or the duration of morphogenesis that result in correlated patterns of accessory cusp expression across molar types. Such individual level influences could be genetic or environmental in origin. For example, genes affecting cusp sharpness could alter the diffusion rates of activators and inhibitors (Jernvall and Jung 2000), changing the size of inhibition zones in a similar way across molar types. Reduction in crown size from nutritional insufficiency could also affect the relationship between intercusp spacing and crown size across an individual's molars.

Because the expression of accessory cusps is determined by upstream events in a developmental cascade, correlations between the Carabelli trait and other dental traits as well as the likelihood of homoplasy may be possible. Developmental correlations between Carabelli and other traits could be perceived to present difficulties in phylogenetic analyses that assume character independence (Kangas et al. 2004). However, at least for UM1s in our studies,

the increased risk of exhibiting an accessory cusp when the Carabelli trait is present is actually quite small. Nevertheless, understanding the developmental basis for Carabelli expression and other dental traits may make it possible to predict with some accuracy patterns of phenotypic expression and coexpression of suites of characters that are likely to arise in evolution (Kavanagh et al. 2007). Understanding the ontogeny of dental features may make it possible to code characters as developmentally significant events rather than as atomized traits (Hunter et al. 2010).

Our study of Carabelli cusp provides a perspective on how a new cusp might arise. Over the evolutionary history of mammals, major dental traits have evolved that began at early evolutionary stages as peripheral features, low on a tooth crown, and developed presumably late in ontogeny. The upper molar hypocone, for example, arose by convergent evolution in many mammalian groups and transformed in some groups into a main cusp approaching the other main cusps (protocone, paracone, and metacone) in size (Hunter and Jernvall 1995). Tribosphenic molars with a protocone or protoconelike cusp may have evolved twice during the Mesozoic in northern-continent tribosphenidans and southern-continent ausktribosphenidans (Luo et al. 2001). Transforming a small, low peripheral cusp into a centrally located, large cusp must be accomplished by shifting initiation of that cusp earlier in ontogeny. Natural selection might drive this heterochronic shift if cusp enlargement results in a new, functionally significant contact with occluding teeth (perhaps explaining why cusps in the Carabelli position have not become major innovations in the mode of the hypocone). However, origin of a new cusp in the first place, to use Carabelli expression as a model, can occur as a by-product of natural variation in the spacing of enamel knots and offset of morphogenesis, which impacts intercusp spacing and tooth size, respectively. Differences in developmental parameters resulting in tooth size increase, with cusp spacing remaining the same, nearly the same, or merely not keeping pace with size increase, seem to be instrumental in establishing a greater probability of Carabelli cusp expression (and likely other accessory cusps) in males than in females, and in UM1 than in UM2 within the same individual. Across species, however, it is likely that multiple developmental parameters must change in a concerted mode, even just to keep shape the same; the reason is that tooth size and cusp spacing appear to be under somewhat separate control.

In sum, we argue that the well-known variations in tooth shape in modern humans, of which Carabelli cusp is a prime example, are explicable in terms of a few simple rules of construction, which in turn derive from the manner in which teeth take on their shape. These morphogenetic rules are universal to mammals and probably nonmammalian vertebrates as well. We have been able to show that variation within individuals, between sexes, and across populations

within a species all follow the same constructional rules. It remains to be seen whether or how these rules will need to be revised and rewritten to account for evolutionary change between species.

4.7 Materials and methods

The samples used in this chapter are housed at the Bioarcheology Laboratory of the OSU Department of Anthropology. The Dayton sample consists of dental casts from Dayton, Ohio, orthodontic patients while the Gullah sample consists of dental casts from the Gullah, African Americans living on St. James Island, South Carolina, during the 1950s (Menegaz-Bock 1968). The casts were made as part of a larger study of Gullah biology and ancestry (Menegaz-Bock 1968). The Seminole sample consists of dental casts from Seminole peoples in Florida. Sample sizes vary for different statistical tests and are given in the results sections of this chapter.

Crown areas, intercusp distances, and Carabelli cusp areas were measured in two dimensions as projected into the occlusal plane using a Hirox digital microscope at a nominal 6× magnification (15 mm × 24 mm field of view). Teeth were oriented by eye so that the widest part of the crown was horizontally level. Crown and Carabelli cusp areas were measured as the areas enclosed within a set of 20–30 points surrounding either the entire crown or Carabelli cusp, respectively.

Carabelli development was also scored using two typological schemes. We employed a simplified scheme labeling Carabelli as ‘‘present’’ where Carabelli area was measurable, ‘‘slight’’ where Carabelli development was evident but not measurable (i.e., not clearly separable from the protocone), or ‘‘absent’’ where Carabelli cusp was not evident whatsoever. We also employed the standardized ASUDAS dental plaque scheme (Turner et al. 1991) coding Carabelli development on a scale from 0 (absent) through 7 (fully independent Carabelli cusp).

We assessed error associated with our measurement protocol in a subsample of 19 teeth measured four times on separate days (Hunter et al. 2010). We calculated a measure of relative measurement error (ME) as a percentage of the total variation among individuals and within individuals (i.e., among replicate measurements of the same individuals) partitioned through Model II ANOVA (Bailey and Byrnes 1990; Yezerinac et al. 1992). Percent ME is more influential than absolute precision of measurements in determining statistical power. ME is moderately high for the linear intercusp distances (12–32 percent), whereas ME is somewhat lower for tooth area (10 percent) and Carabelli area (4 percent). Relatively high ME for the intercusp distances

may be due to the small magnitude of these dimensions (~2–9 mm on average) relative to measurement repeatability (standard error of measurement ~0.20 mm), low variation among individuals due to the functional constraints of precise occlusion, and subjectivity in locating the position of cusp tips. Measuring areas does not suffer from the subjectivity of locating cusp tips, and ME of areas may arise from variation in orienting the teeth relative to the occlusal plane. Because error in measurement should be random, its impact on our statistical tests should be to reduce power, making it more difficult to obtain significant results (i.e., increased type II error). Although methods exist to adjust total variance by removing an estimated proportion of within individual variation (Rohlf et al. 1983), such methods may inflate the probability of obtaining a false positive result (i.e., increased type I error). Instead, we chose to mitigate the potential impact of measurement error on power by analyzing large samples.

Acknowledgments

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5 *The expression of human sex chromosome genes in oral and craniofacial growth*

LASSI ALVESALO

5.1 Introduction

Sexual dimorphism in the growth of bony structures has commonly been attributed to differences in hormonal balance. The action of hormones during puberty has been considered important for expression of this difference, for example, in average adult body height. On the other hand, it has been assumed since the 1960s, on the basis of observations of heights of individuals with sex chromosome anomalies, that human X and Y chromosomes contain genes (determinants) that influence final stature (Ferguson-Smith 1965; Simpson 1976).

Recent results suggest that deletions encompassing a novel homeobox gene within pseudoautosomal regions of the X and Y chromosomes cause growth failure in idiopathic short stature and Turner (45,X females) syndrome (Rao et al. 1997). Investigations of skeletal development in Klinefelter syndrome males and Turner syndrome females indicate that the Y chromosome may possess genes that cause a retardation of skeletal maturation (Tanner et al. 1959). X linkage has been suggested for the rate and timing of ossification (Garn and Rohmann 1962). Dermatoglyphic investigations indicate that sex chromosomes influence fingertip pattern size and the development of the palmar patterns of loops and triradii (Penrose 1968; Polani and Polani 1979). It has also been postulated that the Y chromosome regulates the rate and extent of growth of the primitive gonad (Mittowoh 1985), pointing to a more general regulatory role for this chromosome. Differential ontogenesis of the sexes may depend entirely on a regulatory effect of the Y chromosome as well (Ounsted and Taylor 1972).

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5.2 Tooth crown size

Human dental development begins with formation of the deciduous incisors at about 4 weeks *in utero*, followed by other deciduous and permanent teeth; each passes through a series of well-defined developmental stages. All tooth crowns except the permanent third molars reach their final size and shape between the ages of 2 months and 8 years. Sexual dimorphism in average crown size, with males having larger teeth, is expressed at early and somewhat different stages of development. On the basis of correlative dental studies on normal relatives, X chromosome linkage was proposed for permanent tooth crown size and dental development (Garn and Rohmann 1962; Garn et al. 1965; Alvesalo 1971). The Y chromosome apparently affects crown growth, though its effect differs from that of the X chromosome; as such, sexual dimorphism in average tooth crown size is connected with the influence of the Y chromosome (Alvesalo 1971).

Measurements of total tooth crown sizes in dental casts from individuals with various sex chromosome anomalies show that permanent and deciduous teeth of 47,XYY males and permanent teeth of 47,XXY males are generally larger than those of normal 46,XY males (Alvesalo et al. 1975; Alvesalo and Kari 1977; Alvesalo and Portin 1980; Townsend and Alvesalo 1985a, 1985b). In contrast, permanent and deciduous teeth of 45,X females and permanent teeth of 45,X/46,XX females (i.e., with one X and normal XX cell lines) and 46,Xi(Xq) females (one normal X and one isochromosome with the long arm duplicated) are smaller than those of normal 46,XX females (Filipsson et al. 1965; Kari et al. 1980; Townsend et al. 1984; Mayhall and Alvesalo 1992; Mayhall et al. 1991; Varrela et al. 1988). Females with the complete form of testicular feminizing syndrome, or 46,XY females, who are insensitive to androgens, have teeth of similar size to normal males (Alvesalo and Varrela 1980). These results help establish the growth-promoting effects of X and Y chromosome genes on tooth crown size. They operate early and apparently in a continuous manner during dental development. The location of the growth promoting region within the X chromosome is probably on the short arm (Mayhall et al. 1991); that on the Y chromosome may be on the proximal, nonfluorescent portion of the long arm (Alvesalo and de la Chapelle 1981). As for the timing of dental development, present knowledge is limited to Turner females, who show advanced permanent tooth eruption and maturation compared to normal females (Filipsson et al. 1965; Kari and Alvesalo 1985; Kari et al. 2011; Midtbø and Halse 1992). Unpublished data further confirm the results in Turner females (45,X) and indicate delayed dental development in 47,XYY males (Kari et al. 2011).

5.3 Tooth crown structure

The distance across the dentinoenamel junctions is determined at an early stage of tooth crown development, at the time when amelogenesis or enamel formation is beginning. Mitotic activity of cells of the inner enamel epithelium is the decisive factor in determining this distance (Kraus and Jordan 1965). Enamel thickness provides a measure of the secretory activity of postmitotic, highly differentiated ameloblasts, whereas dentin thickness reflects growth due to mitotic activity in the developing tooth germs. Measurements of enamel and dentin thickness on radiographs of maxillary permanent incisors, canines, and molars in normal females and males; 45,X, 45,X/46,XX, and 47,XXX females; 47,XYY and 47,XXY males; and 46,XY females demonstrate that the Y chromosome influences dental growth by promoting both amelogenesis and dentinogenesis (Alvesalo 1985; Alvesalo and Tammisalo 1981; Alvesalo et al. 1985, 1987, 1991; Zilberman et al. 2000). It is conceivable that the mitotic potential is increased in the presence of the Y chromosome, which leads to an increase in cell division at various developmental stages (Alvesalo and Tammisalo 1981; Alvesalo et al. 1991; Zilberman et al. 2000). The X chromosome exerts its influence on crown enamel deposition or it contains an enamel gene; however, it has little or no influence on the growth of crown dentin. Enamel genes, conceivably structural by their function, in both X chromosomes of normal females and all three of 47,XXX females are active, possibly continuously so or at least intermittently. The effect of the X chromosome on metric enamel growth is similar in magnitude to that of the Y chromosome, though there is a trend for the greater expression of X chromosome influence. Pedigree studies have shown that in addition to various forms of autosomally inherited amelogenesis imperfecta or heritable defective development of tooth enamel, one hypoplasia type of this defect also shows X-linked dominant inheritance. Therefore, finding an enamel gene on the X chromosome was not entirely unexpected (Alvesalo and Tammisalo 1981; Figures 5.1–5.4).

Until recently, there have not been any pedigree studies (e.g., Y-linked amelogenesis imperfecta) or other indications of the presence of specific enamel genes on the Y chromosome. This and other factors suggest the regulative nature of tooth growth genes on the Y chromosome, at least with respect to enamel formation (Alvesalo 1985). It is therefore of interest that molecular studies show that the gene loci for human amelogenin, which is the main protein component of enamel organic matrix, are on both the X and Y chromosomes (Lau et al. 1989; Nakahori et al. 1991; Salido et al. 1992). Amino acid sequences of these X and Y amelogenin genes differ to some extent, and transcriptional products of the X and Y chromosomes are quantitatively and qualitatively different. The Y chromosome locus encodes a functional protein

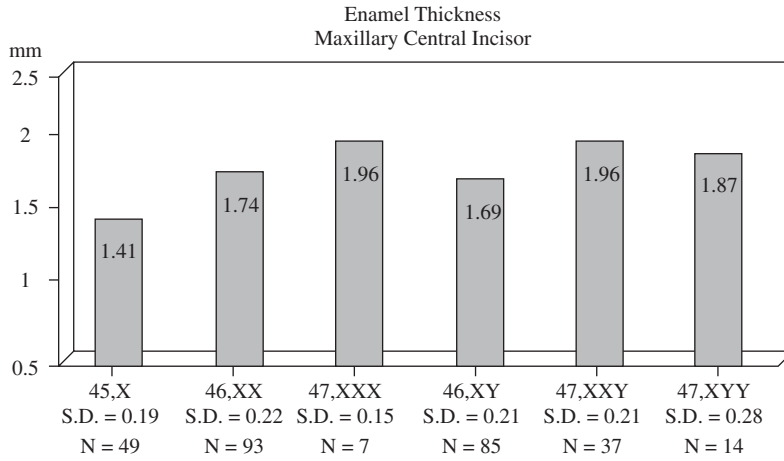

Figure 5.1. Mean enamel thickness (mesial enamel layer plus distal enamel layer) of the maxillary permanent central incisors of normal 46,XX females, normal 46,XY males, and individuals with various sex chromosome anomalies, including 45,X and 47,XXX females and 47,XXY and 47,XYY males. Enamel thicknesses were determined from standardized intraoral radiographs. P value < 0.0001 in one-way analysis of variance. 45,X female: female with one X chromosome; 47,XXX female: female with an extra X chromosome; 47,XXY male: male with an extra X chromosome; 47,XYY male: male with an extra Y chromosome.

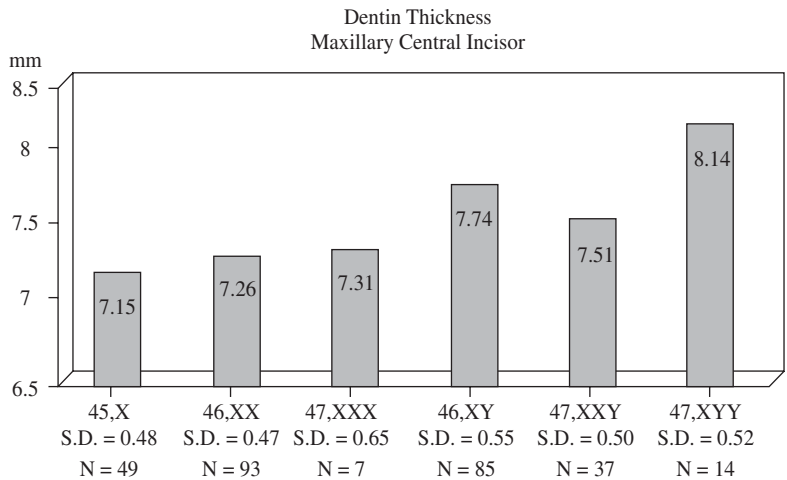

Figure 5.2. Mean dentin thickness (maximum mesiodistal dimension of tooth crown minus enamel layers) of the maxillary permanent central incisors of normal 46,XX females, normal 46,XY males, and individuals with various sex chromosome anomalies, including 45,X and 47,XXX females and 47,XXY and 47,XYY males. Determinations were made from standardized intraoral radiographs. P value < 0.0001 in one-way analysis of variance.

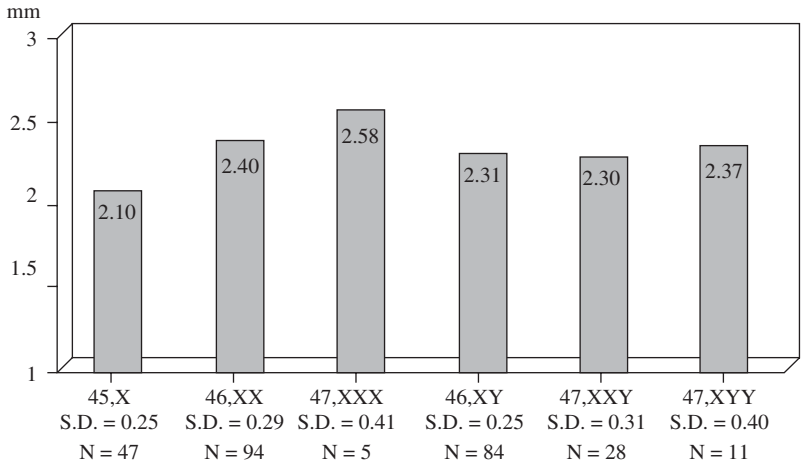

Figure 5.3. Mean enamel thickness (mesial enamel layer plus distal enamel layer) of the maxillary permanent canines of normal 46,XX females, normal 46,XY males, and individuals with various sex chromosome anomalies, including 45,X and 47,XXX females and 47,XXY and 47,XYY males. Enamel thicknesses were determined from standardized intraoral radiographs. P value < 0.0001 in one-way analysis of variance.

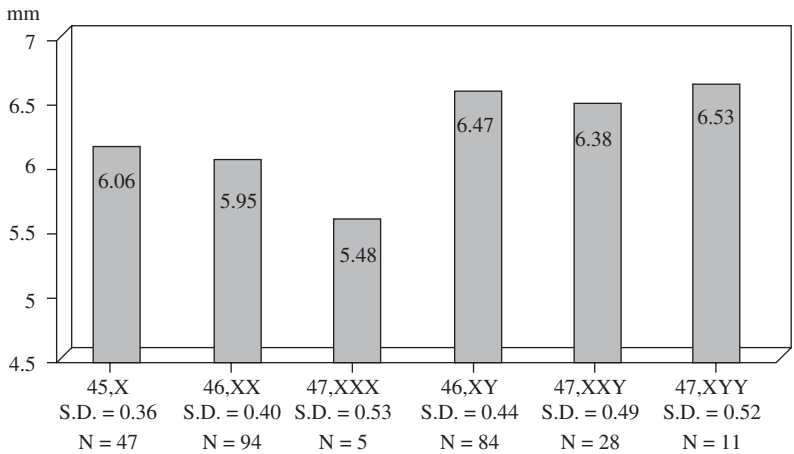

Figure 5.4. Mean dentin thickness (maximum mesiodistal dimension of tooth crown minus enamel layers) of the maxillary permanent canines of normal 46,XX females, normal 46,XY males, and individuals with various sex chromosome anomalies, including 45,X and 47,XXX females and 47,XXY and 47,XYY males. Determinations were made from standardized intraoral radiographs. P value < 0.0001 in one-way analysis of variance.

even though its level of expression is only 10 percent that of the locus on the X chromosome (Salido et al. 1992). These genes are located on the distal short arm of the X chromosome and possibly the proximal long arm region of the Y chromosome (Lau et al. 1989). The short arm of the Y chromosome is a possible location for the amelogenin gene (Nakahori et al. 1991; Salido et al. 1992). Running counter to molecular results, it is of interest that for X-linked amelogenesis imperfecta in males, the enamel is extremely thin and smooth, whereas for females the enamel is almost of normal thickness but with defective vertical ridging.

5.4 Tooth root size

Permanent tooth root lengths measured on radiographs in 47,XYY and 47,XXY males were longer than in normal men and women; roots in the 45,X/46,XX females were shorter. Root lengths of 46,XY females were similar to those of normal men. The root lengths of the canines, maxillary central incisors, and mandibular lateral incisors clearly differed among normal men, women, and 45,X/46,XX females; men had the longest roots, mosaic females the shortest, and normal women had intermediate root lengths. This length in all teeth differed between the mosaics, that is, 45,X/46,XX females and the trisomies 47,XXY and 47,XYY males (Lähdesmäki and Alvesalo 2004, 2007). Permanent root lengths in 45,X and 46,Xi (Xq) females were also shorter than in normal women (Filipsson et al. 1965; Midtbø and Halse 1994). It appears that the X chromosome has a definite effect on root dentin growth, in contrast to its effect on crown dentin growth.

Root lengths in the population control males were longer than those in population control females (Lähdesmäki and Alvesalo 2004), as observed previously on measurements of natural teeth (Selmer-Olsen 1949). The mean difference between the sexes was 5 percent (Lähdesmäki and Alvesalo 2004), which is similar to the 6 percent reported by Garn et al. (1978) for mandibular canines, premolars, and molars. The preceding studies (Lähdesmäki and Alvesalo 2004, 2007) indicate the promoting effect of the Y chromosome on growth in root length is greater than that of the X chromosome, which may lead to sexual dimorphism in root size. It has been suggested that X and Y chromosome genes affecting crown growth are also expressed in the following root dentin growth. Recent research on 47,XXX females (Lähdesmäki and Alvesalo 2010) indicates increased tooth length relative to that in normal females. Also shown is an increase in the expression of taurodont teeth, which parallels earlier findings on individuals with extra X chromosomes (Varrela et al. 1988; Varrela and Alvesalo 1989).

5.5 Tooth crown shape

Crown morphology in 47,XYY males is changed, in that the degree of UI2 shoveling is greater, and the palatal fossa deeper than in their relatives. For 45,X females, UI2s are less shovel-shaped than in normal women, and UI1s have a shallower fossa; in addition, there is a tendency for fewer cusps and simplified crown shapes in the molars (Kirveskari and Alvesalo 1981, 1982; Midtbø and Halse 1994). Midtbø and Halse (1994) found an altered mammelon pattern in Turner women, especially on the incisal edge of the UI2s, together with atypical mesiobuccal cusps and nippled cusp tips of the UC, UP1, and UP2. Carabelli's trait on UM1 was far less common than in a normal Finnish population (Alvesalo et al. 1975; Midtbø and Halse 1994; Nakayama et al. 2005, 2011; Scott and Turner 1997).

Sex chromosomes have an effect mainly on the cusp basal area rather than cusp height. The basal area is smallest in 45,X females, with the sharpest cusps; it becomes larger in normal women and men and is even larger in 47,XYY males – who have the bluntest cusp forms (Mayhall and Alvesalo 1995). Unpublished data suggest additional X chromosome material in 47,XXX and 48,XXXX females causes a higher frequency of Carabelli's trait (Nakayama et al. 2011). It appears that sex chromosomes have a definite effect on cusp shape and size in all three dimensions but may not influence the developing cusps and teeth equally; this influence may be due to the varying contribution of enamel and dentin to different measures (Mayhall and Alvesalo 1995; Pirttiniemi et al. 1998).

5.6 Cephalometric craniofacial pattern

45,X females have marked changes in relatively few craniofacial areas. Most changes are located in the cranial base, so that the face is retrognathic. The mandible is short, whereas the maxilla is of normal length. These results support the view that morphology of the cranial base is markedly affected in 45,X females, whereas most other craniofacial changes could be considered secondary. Retarded cartilage growth may help explain these findings (Peltomäki et al. 1989). Moreover, the reduction of sex chromosome genetic material in 45,X/46,XX or mosaic Turner females results in the reduced craniofacial dimension, affecting dimensional ratios and especially plane angles of the cranial base (Grön 1999).

In 47,XXX females, lengths of the anterior and posterior cranial base, the calvarium, mandibular ramus, and posterior and upper anterior face heights were significantly shorter than in normal female controls. Angles between the

foraminal and clival planes, mandibular plane and cranial base, maxillary and occlusal planes, maxillary and mandibular planes, and foraminal and mandibular planes, as well as the gonial angle, were significantly enlarged (Krusinskiene et al. 2005).

Compared with female relatives, 47,XXY males were larger in almost all craniofacial linear dimensions but were similar in facial shape apart from greater mandibular prognathism. Mandibular dimensions in particular differed between Klinefelter and unaffected males; the corpus length was larger, the ramus shorter, and the gonial angle more obtuse in the 47,XXY group. For craniofacial size, the majority of mean values fell between those of males and females. The prominent facial profile, most marked in the mandible, was a dominant feature of Klinefelter subjects, who also displayed a more acute median cranial base angle than each control group. Generally, Klinefelter morphology was marked by greater variability in patterning of craniofacial structures compared with relatives – possibly due to decreased developmental canalization. The 47,XXY complex may affect endochondral growth in the cranial base, as well as have a direct influence on jaw growth (Nakayama et al. 2011).

The supernumerary Y chromosome in 47,XYY males results in larger craniofacial dimensions than in normal males, without substantial effects on dimensional ratios and plane angles. This general metric pattern is similar to that in many adult body and head dimensions as well as dental arches and tooth crowns. The foramen magnum in 47,XYY males was smaller in the sagittal plane than in normal males and females (Krusinskiene et al. 2005). The findings of reduced linear measurements in 47,XXX females, together with results of studies on the craniofacial complex of 47,XXY and 47,XYY males, suggest that dimensional variation between groups results from the promoting effect of an extra Y chromosome and retarding effect of an extra X chromosome (Brown et al. 1993; Grön 1999, Grön et al. 1997; Krusinskiene et al. 2005).

5.7 Occlusion

Turner patients and females with X chromosome anomalies such as 45,X, 45,X/46,XX, and 46,Xi(Xq) have an increase in class II malocclusions, lateral crossbites, and anterior open bite (Alvesalo and Laine 1992; Harju et al. 1989; Laine et al. 1986, 1992; Midtbø and Halse 1996). Studies of occlusion in 47,XXY men show that mesial molar occlusion is a relatively frequent anomaly, and that incisal open bite is more common than in controls (Laine et al. 1986). The 47,XYY men, like 47,XXY, have mesial molar occlusion and mandibular overjet more often than other groups (Laine et al. 1992). 45,X women

clearly have the highest frequency of distal occlusion and large overjet. The 47,XXY men have the highest frequency of most typical occlusal anomalies.

5.8 Palatal morphology

Some researchers report a high palate in Turner individuals (45,X women) while others find normal palatal height but decreased width and lateral palatine ridges (Laine and Alvesalo 1993; Perkiömäki and Alvesalo 2007). 47,XXY males tend to have a shallower but longer palate than normal men; their palate is also narrow. The mandible is narrower but sagittally longer relative to the mandibles of normal men. Results indicate the presence of one extra X chromosome in 47,XXY men is reflected in decreased growth of the maxilla transversely and vertically, and of the mandible transversely. Increased length of the alveolar arches might partly compensate for the decreased width of the alveolar arch. This change might be associated with larger tooth size in 47,XXY men (Laine and Alvesalo 1993).

Compared to normal males, in 47,XYY males the extra Y chromosome causes an increase in palatal growth transversely and anteroposteriorly, and in mandible arch length anteroposteriorly. Palatal height and mandibular width are smaller with this chromosome pattern. Findings in 47,XYY men are in accordance with earlier observations that the palate becomes shallower with the addition of a sex chromosome. It is also apparent that the influence of X and Y chromosomes differs, at least regarding magnitude of metric changes (Laine et al. 1992). In general, an increase in the number of sex chromosomes is associated with changes in palatal and mandibular arch dimensions.

5.9 Torus mandibularis and palatinus

Ninety-three 45,X Finnish females were examined to determine the frequency and expression of torus mandibularis, a bony exostosis on the lingual surface of the mandibular corpus. Among adults, results show that trait frequency is significantly lower and expression weaker compared with male control relatives. A similar pattern was observed in comparisons to normal female relatives. These findings suggest sex chromosomes may have an influence on the occurrence, expression, and timing of torus development. Sexual dimorphism in the manifestation of torus mandibularis as observed in the Hailuoto population (Alvesalo and Kari 1972) may result from the effect of the Y chromosome (Alvesalo et al. 1996). Early growth of tori in the 45,X females seems to be on pace with the advanced dental development rather than with growth of the facial or postcranial

skeleton (Alvesalo and Kari 1972; Alvesalo et al. 1996; Filipsson et al. 1965; Tanner et al. 1959). Female predominance has often been reported for the occurrence of torus palatinus [e.g., Hailuoto population in Finland (Kari and Alvesalo 1973)]. Unpublished data on torus occurrence in 47,XXY males suggest a clear increase compared to control males and females (Perkiömäki and Alvesalo 2011).

5.10 The expression of sexual dimorphism

In genetic texts, sex-influenced inheritance traditionally refers to the more frequent expression of autosomal genes in one sex, although hormonal influence has been considered important in this respect as well. Missing and supernumerary teeth, familial features that possibly show dominant autosomal transmission, are dental examples of this phenomenon. Supernumerary permanent teeth are approximately twice as common in normal males as in normal females, while ordinary teeth are missing more often in females. It has been suggested that these differences can be explained by differential effects of the X and Y chromosomes on dental growth; it is particularly likely that the Y chromosome increases mitotic activity within the developing dental lamina, from which the teeth germinate (Alvesalo 1997; Kraus and Jordan 1965). These effects can also explain other sexual differences in the dentition, including (1) sexual dimorphism in average permanent tooth crown size, which is decisively due to dentin thickness (Alvesalo 1985, 1997; Harris and Hicks 1998); (2) tooth root dentin size (Lähdesmäki and Alvesalo 2004); (3) tooth crown morphology, where even the shape of tooth cusps in males seems to differ from that in females (Mayhall and Alvesalo 1995; Pirttiniemi et al. 1998); and (4) developmental timing of the permanent teeth, where an increase in total tooth substance in males may relate to retardation of their dental development relative to females (Alvesalo 1971; Laine et al. 1992; Figure 5.5).

Assuming genetic pleiotropy, in that the effect of the X and Y chromosomes on cell secretory function and proliferation are not limited to the teeth, sexual dimorphism in torus mandibularis (Alvesalo and Kari 1972; Alvesalo et al. 1996), skeletal maturation (Alvesalo 1971; Alvesalo et al. 1991), and statural growth may also be explained by their differential action. The sex ratio at birth, as well as in the earlier stages of development, may also relate to increased mitotic potential from the Y chromosome (Alvesalo 1985; Alvesalo and Tammisalo 1981; Figure 5.5). There is a significant change in sex ratio with increasing duration of pregnancy. For example, in a Finnish study of 551 conceptuses from induced abortions, the embryonic sex ratio was as high as 164 and the fetal ratio 111; the mean sex ratio at birth in Finland was only

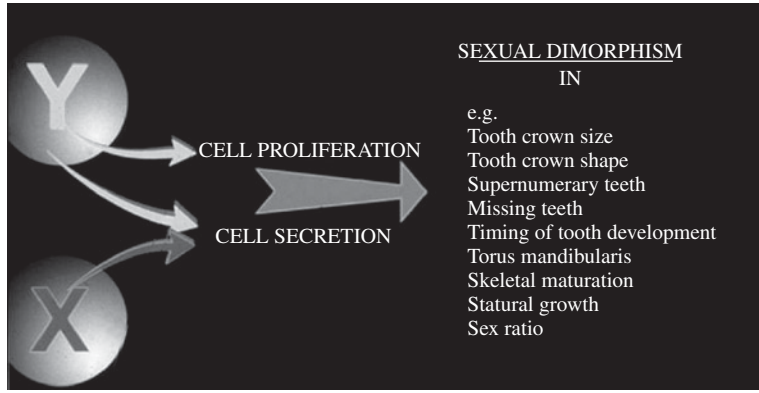

Figure 5.5. A schematic model describing differential effects of the human X and Y chromosomes on tooth crown growth and resulting expression in somatix sexual dimorphism. An assumption of genetic pleiotropy of these effects is made regarding torus mandibularis, statural growth, skeletal maturation, and sex ratio.

105 (Kellokumpu-Lehtinen and Pelliniemi 1984). It seems that the 46,XY chromosome complement makes for a better start than the 46,XX constitution (Alvesalo 1997; Park et al. 1983).

5.11 Summary and prospects

Studies on tooth crown size and structure in families and in individuals with various sex chromosome anomalies have demonstrated differential direct effects of human X and Y chromosome genes. The Y chromosome promotes tooth crown enamel and dentin growth, whereas the effect of the X chromosome on crown growth seems to be restricted to enamel formation. Enamel growth is decisively influenced by cell secretory function and dentin growth by cell proliferation. The differential effects of the X and Y chromosomes on growth may explain the expression of sexual dimorphism in various somatic features. Examples include tooth crown and root size, crown shape, the number of the teeth, and, under the assumption of genetic pleiotropy, torus mandibularis, statural growth, and sex ratio. Molecular studies show that the gene loci for human amelogenin, the major protein component of the organic matrix in enamel, are on both the X and Y chromosomes.

Several questions remain regarding the manner and extent of influence of the Y chromosome tooth growth gene(s). Does the increase in mitotic potential promote penetrance of normal genes or inhibit defective genes involved in dental development, for instance, leading to sexual dimorphism in the number of the

teeth? Does the Y chromosome wake up "sleeping" genes in males, leading to greater expression of atavistic features in the form of supernumerary teeth? Is the Y chromosome involved in the mineralization process? Are enamel and dentin growth regulated by the same tooth growth gene? What is the role of the Y chromosome in uncontrolled growth? These questions will be pursued in the analyses of deciduous and permanent teeth that I have received from individuals with various sex chromosome anomalies and their first-degree female and male relatives (Alvesalo 1997, 2009).

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6 *Significant among-population associations found between dental characters and environmental factors*

YUJI MIZOGUCHI

6.1 Introduction

To some extent, we know how genes control or influence morphological structures during ontogeny. Recent research in genetics and molecular biology has identified genes underlying various characters, including morphological traits (Bianchi et al. 2007; Coussens and van Daal 2005; Dorus et al. 2004; Fujimoto et al. 2008; Kimura et al. 2009; Medland et al. 2009; Mustonen et al. 2003; Pickrell et al. 2009; Sabeti et al. 2007; Tabata 2004; Tucker et al. 2004). Among others, *EDA, EDAR,* and *EDARADD* genes in the ectodysplasin signaling pathway are involved in tooth development (Mustonen et al. 2003; Sabeti et al. 2007; Tabata 2004; Tucker et al. 2004). Kimura et al. (2009), using two Japanese samples, attempted to clarify the association between a nonsynonymous-derived variant, 1540C (rs3827760), in the ectodysplasin A receptor gene (*EDAR* [MIM 604095]), and shoveling of the maxillary central incisor. They found the number of *EDAR* 1540C alleles in an individual was strongly correlated with grade of shoveling. In another report on dental morphogenesis, Bianchi et al. (2007) examined unrelated individuals of European origin with hypodontia and control individuals without hypodontia. Their results suggested that third molar agenesis is associated with promoter polymorphisms (G-915C) of the *PAX9* gene, mutations that had been shown to be associated with autosomal dominant forms of oligodontia (agenesis of more than six teeth, MIM 604625).

When did such genes appear and become fixed in ancestral populations? Although studies of genomewide scans for positive selection (Pickrell et al. 2009; Pritchard 2010; Sabeti et al. 2007) are progressing, so far they only

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indicate the existence of natural selection for a few single nucleotide polymorphisms (SNPs) in some genes and/or relative among-population variations in SNPs as expressed by Wright's F_{ST} (Relethford 1994). Even if the correspondence of genes to their functions were elucidated in molecular biology, it would be impossible to determine the cause of their appearance and fixation if we only explore genes in living human populations. To clarify the mechanisms underlying the relationship between natural selection and dental morphology, we must collect data on ancient environments where morphological characters and their associated genes first came into existence. At present, however, we do not have sufficient paleoecological data to achieve this aim. Instead, we are obliged to use data on environments inhabited by modern humans, under the assumption that there have been no dramatic changes for the past few hundred thousand years.

Since 1985, the author has attempted to estimate the degree of among-population correlations between dental characters and environmental factors to explore the causes underlying their variation and existence. Here, the results of these attempts are outlined. Models aimed at solving this problem in the future are also discussed.

6.2 Previous studies on among-population associations

6.2.1 Dental characters and environmental factors

The premise adopted here is that the appearance and fixation of morphological characters (or gene/genes) in our ancestral populations resulted from adaptations to environmental factors and did not simply appear by chance. Following this premise, I have compared geographical patterns of variation for some dental morphological characters to environmental factors to determine whether there is any evidence to support the notion that these characteristics are adaptive. Among-population (or interpopulation or ecological) associations between traits and environmental factors were quantitatively assessed using rank correlation coefficients or multivariate analyses (e.g., principal components and canonical correlation analyses).

The first trait evaluated for its potential adaptive significance was the classic morphological trait shovel-shaped incisors. Using twenty-two pooled samples, I found shoveling had a significant positive association with latitude and a negative association with average annual temperature. Further, there appeared to be an inverse correlation with subsistence strategies that focused on milking (Mizoguchi 1985). These findings, along with previous studies on the facial structure of Inuits and the food habits of hunter-gatherers, suggested

that shoveling was a component of the facial structures that resisted powerful biting forces. The need for a powerful biting mechanism was apparently tied to subsistence hunting with its heavy reliance on meat eating.

Following the analysis of shoveling, I focused on the correlations between Carabelli trait and various environmental factors (Mizoguchi 1993a). Findings suggested that people whose subsistence focused on milking in dry and slightly cold regions tended to have well-developed Carabelli cusps, buccolingually smaller molars, and a narrower nose, along with relatively weak expressions of incisor shoveling. The inference is that the Carabelli trait on the UM1 had been caused, first, by a reduction of the molar itself and, then, by remaining biomechanical stresses on the molar tooth that focused on the loci where Carabelli is expressed.

Interpopulation associations have also been evaluated for tooth crown size and the types of food consumed by different populations (Mizoguchi 1993b). Canonical correlation analyses of male and female samples from various regions in the world suggest that people who traditionally consumed more wheat and eggs had smaller permanent teeth in general. If the same amount of nutrients can be utilized by eating more nutritious foods with smaller teeth, then smaller teeth are presumably more advantageous than larger teeth from the standpoint of metabolic economy (Bailit and Friedlaender 1966).

Although the preceding findings are suggestive, there is still no direct evidence that dental characters reflect an adaptation to particular environmental stresses, as noted by Hlusko (2002) in her paper on cingular remnants. Scott and Turner (1997) are of the opinion that geographical variations in dental morphological traits are largely generated by the random processes of founder effect and genetic drift. However, there is no definitive evidence that chance is the cause of the appearance and variation shown by nonmetric tooth crown and root characters. This point should be explored further.

6.2.2 Geographic clines in biochemical/physiological characters

In support of the aforementioned among-population associations between dental characters and environmental factors, it is widely known that genes for biochemical and physiological characters, such as the ABO and Rh blood-group systems, hemoglobin S, beta-thalassemia, glucose-6-phosphate dehydrogenase, alpha-2HS-glycoprotein, and so on, show geographical clines in their frequencies or have ecological correlations with latitude and/or climatic factors (Cavalli-Sforza and Cavalli-Sforza 1995; Ciminelli et al. 2000; Lewontin 1995; O'Rourke et al. 1985; Piazza et al. 1981; Spitsyn et al. 1998). Some of these clines or correlations have been interpreted as the result

of gene flow or migration, while others have been explained as adaptations to various environmental stressors. This is particularly true for hemoglobinopathies, which are strongly associated with malaria. If any associations are found between biochemical/physiological and dental characters, we may be able to understand the reason for the appearance and maintenance of various tooth crown and root traits.

6.3 Character complexes: dental and biochemical/physiological characters

At present, we have little direct evidence that natural selection is responsible for the presence and patterns of variation of dental morphological characters. But, at least, the signaling pathway involved with *EDAR* has probably been a target of selection. Pickrell et al. (2009) stated that this was one of only a few examples where a signal for selection had been successfully linked to a phenotype. Given such circumstances, it seems worthwhile to examine further the associations between morphological and biochemical/physiological characters.

The present author had been interested in seeking the causes of adaptive evolution before recent researchers began using selective sweeps across SNPs. Therefore, I examined the possibility that some biochemical/physiological characters, whose genes may be involved in the ontogenetic process influencing the expression of a dental morphological character, support the existence of the morphological character in certain natural or cultural environments (Mizoguchi 1994, 2006). The results are summarized as follows.

The characters compared include five tooth crown diameters, two nonmetric dental characters, and thirty-seven alleles for biochemical/physiological characters (Mizoguchi 2006). Dental data are represented by mean values or frequencies compiled by Mizoguchi (1985, 1993a), while biochemical data take the form of allele frequencies for various polymorphic genes for enzymes, proteins, blood groups, etc. (Roychoudhury and Nei 1988). Environmental variables that were compared with dental and biochemical characters include climatic and cultural variables, the latter of which reflect "way of life" from the fifteenth century (Ishige 1973). Using these data, twenty-one pooled samples for various regions in the world were created for among-population analyses.

Using Kendall's rank order correlation coefficient, Mizoguchi (2006) found that many genetic markers showed significant correlations with seven metric and nonmetric dental characters (0.05 level). Significant correlations were found between (1) mesiodistal (MD) crown diameter of the UI1 and five alleles, (2) MD crown diameter of the UM1 and six alleles, (3) MD crown

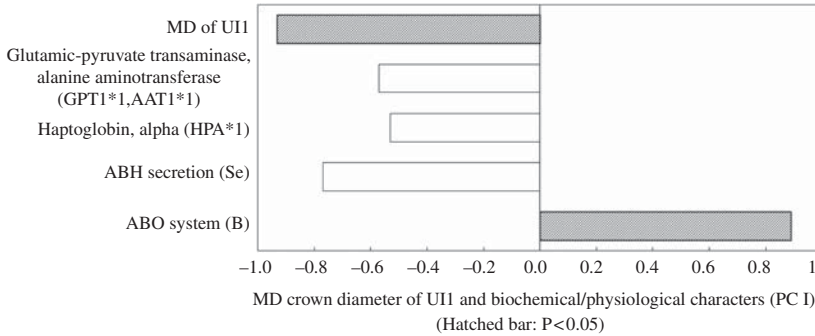

Figure 6.1. Factor loadings on the first principal component from the data set of the mesiodistal crown diameter of the maxillary central incisor and biochemical/physiological characters. Data source: Mizoguchi (2006).

diameter of the UM2 and six alleles, (4) buccolingual (BL) crown diameter of the UM1 and four alleles, and (5) BL crown diameter of the UM2 and three alleles. For the two nonmetric crown traits, UI1 shoveling was associated with nine alleles while UM1 Carabelli's trait was associated with three alleles.

The second step of the analysis involved the use of principal components (Lawley and Maxwell 1963; Okuno et al. 1971, 1976; Takeuchi and Yanai 1972) and Kaiser's normal varimax rotation method (Asano 1971; Okuno et al. 1971). Using these techniques, Mizoguchi (2006) found some indication of character complexes consisting of dental and biochemical/physiological characters. Among others, the following connections were confirmed by the bootstrap test (Diaconis and Efron 1983; Efron 1979a, b, 1982; Mizoguchi 1993b) to be significant at the 0.05 level: (1) an inverse association between the MD diameter of UI1 and allele B of the ABO system (Figure 6.1); (2) positive associations between the MD diameters of UM1 and UM2 and allele 1 of haptoglobin-alpha, allele S of properdin factor B glycine-rich beta-glycoprotein, and allele Se of the ABH secretion, as well as an inverse association with allele B of the ABO system; and (3) a positive association between shoveling and cDE of the Rhesus system.

Principal components analyses (PCAs) and rotated solutions showed several putative character complexes were significantly associated with natural or cultural environmental factors (Mizoguchi 2006). The main findings are as follows.

6.3.1 Mesiodistal crown diameters and the ABO-blood group system

Although inverse associations were found between the MD diameters of UI1, UM1, and UM2 and allele B of the ABO system in the second-step analysis, the associations of this putative character complex with climatic variables

or ways of life were not significant in the final-step analyses. However, the strong connection between allele B and dental size is interesting. As for the distribution of allele B, the frequency decreases from Central Asia to western Europe, and to the Americas via China and Alaska, and Australia, where allele B is virtually absent in Native Americans and Native Australians (Dobzhansky 1963; Hoshi 1977; Lewontin 1995; Marks 1995; Mettler and Gregg 1969; Stern 1960). This fact is consistent with the findings of the second-step analyses (Mizoguchi 2006), which show that allele B is rarely observed in people with very large teeth, including Native Americans and Australians. The lack of allele B in the Americas is generally considered to be a result of genetic bottlenecking (Komai 1966). Stern (1960), however, stated that there remained the slight possibility of a gradient in blood-group alleles reflecting not only gene flow but unknown selective influences that follow a geographic gradient. The significant among-population associations found by Mizoguchi (2006) may support another explanation for this lack of allele B in the Americas or Australia as dental size is controlled by polygenes that are not affected as much by genetic drift.

6.3.2 Mesiodistal crown diameters and haptoglobin-alpha

The MD diameters of UM1 and UM2 were also found to be associated with many biochemical/physiological characters in the second- and final-step analyses (Mizoguchi 2006). The putative character complex consisting of haptoglobin-alpha allele 1 (HPA*1 or HP*1) and the maxillary molar MD diameters was significantly associated with a climatic factor, that is, average temperature in the coldest month (Figure 6.2). For HP*1, Piazza et al. (1981) reported that it has a relatively high inverse correlation with latitude, and Cavalli-Sforza et al. (1994) have shown it has a relatively high positive correlation with humidity/rainfall. Further, haptoglobin may have some association with malaria (a.k.a. "swamp fever") due to the relatively high frequency of HP 1–1 individuals (homozygous for HP*1) in areas with high rates of hemolysis due to malaria, including Africa (Harrison et al. 1977; Hoshi 1977). In contrast, it is known that the frequencies of HP*1 are conspicuously low in parts of Asia where such hemolysis is equally common (Harrison et al. 1977). Mizoguchi's (2006) finding that the frequency of HP*1 tends to be high in hot regions (Figure 6.2) is consistent with the report on latitude by Piazza et al. (1981) and, partly, with the description of malaria by Hoshi (1977) and Harrison et al. (1977). The association of HP*1 with average temperature in the coldest month is not as strong, and the association with latitude is not significant (Figure 6.2). Therefore, associations of HP*1 with latitude, temperature, humidity/rainfall, and malaria must be evaluated further.

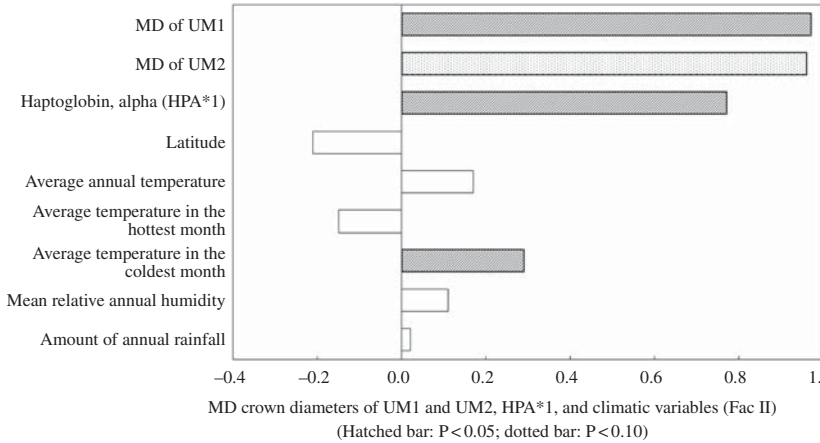

Figure 6.2. Factor loadings on the second rotated factor from the data set of the mesiodistal crown diameters of the maxillary first and second molars, haptoglobin-alpha allele 1, and climatic variables. Data source: Mizoguchi (2006).

6.3.3 Buccolingual crown diameters and the MNS blood-group system

The BL diameters of UM1 and UM2 did not show any significant associations with biochemical/physiological characters in the second-step analyses (Mizoguchi 2006). In the final-step analysis, the BL diameter of UM2 and alleles MS of the MNS system were inversely associated with each other; this putative character complex was further associated (in the case of UM2, positively, and MS, negatively) with average annual temperature, average temperature in the hottest month, average temperature in the coldest month, and amount of annual rainfall. The cause of this is possibly not due to genetic drift but adaptation to the same environmental factors such as temperature and rainfall, or due to gene flow, because dental size seems less affected by genetic drift.

6.3.4 Shoveling and the Rhesus blood-group system

UI1 shoveling was significantly associated with *cDE* of the Rhesus system (RH*cDE) in the second-step analysis (Mizoguchi 2006). In the final-step analysis, this putative character complex was not significantly associated with any natural or cultural environmental variable (Mizoguchi 2006). It has been reported, however, that UI1 and/or UI2 shoveling has significant positive correlations with latitude and significant inverse correlations with temperature (Mizoguchi 1985). Similarly, RH*cDE has a relatively high positive correlation

with latitude (Piazza et al. 1981) and a strong inverse correlation with temperature (Cavalli-Sforza et al. 1994). Therefore, there remains the possibility that the ecological association between these two characters is not due to genetic drift but to adaptation to common environmental factors such as temperature.

6.3.5 Shoveling and lactase activity

Lactase activity had a significant inverse correlation with shoveling at the 0.01 level in the first-step analysis (Mizoguchi 2006). However, the second-step and final-step analyses did not support this putative character complex, probably because of the small number of populations sampled. It is interesting, however, that this character complex seems to be associated with cattle breeding and milking in the PCA on cultural environmental factors for the final-step analysis (the factor loadings on PC 1 are 0.74 for shoveling, –0.69 for lactase activity, –0.77 for cattle breeding, and –0.71 for milking). Lactase activity remains high even in adult Europeans and other regions with a history of dairying (Dobzhansky et al. 1977; Jones 1992; Marks 1995). This is considered to be the result of adaptation to milk use (Dobzhansky et al. 1977; Molnar 1992). Boaz and Almquist (1997) believe the type of lactose intolerance in most modern humans may be an adaptation that prevents adults, who can eat foods other than milk, from directly competing with their young for nourishment. Although the earlier putative character complex of nonshoveling and lactase activity was not shown to have significant associations with cattle breeding and milking (Mizoguchi 2006), these previous studies support the strong connection between such a character complex and subsistence lifeways that involve milking. If so, the inverse association between shoveling and lactase activity may not be caused by genetic drift but by parallel adaptations to environmental factors such as milking.

6.3.6 Carabelli trait and the Kidd blood-group system

A few character complexes that included the Carabelli trait of UM1 were suggested in the second-step analyses, but their existence was not statistically significant (Mizoguchi 2006). In the final-step analyses, however, Carabelli trait and allele Jk*a of the Kidd system constituted a putative complex that might be associated with hunting-gathering (Figure 6.3) or milking (Figure 6.4). The former association was shown by PC 1 and the latter, by the first rotated factor (Fac 1). In general, hunting-gathering is inversely associated with cattle breeding or milking; this association is, in fact, suggested by PC 2 and Fac 2 from the same PCA and rotated solution, respectively (Mizoguchi 2006). Therefore,

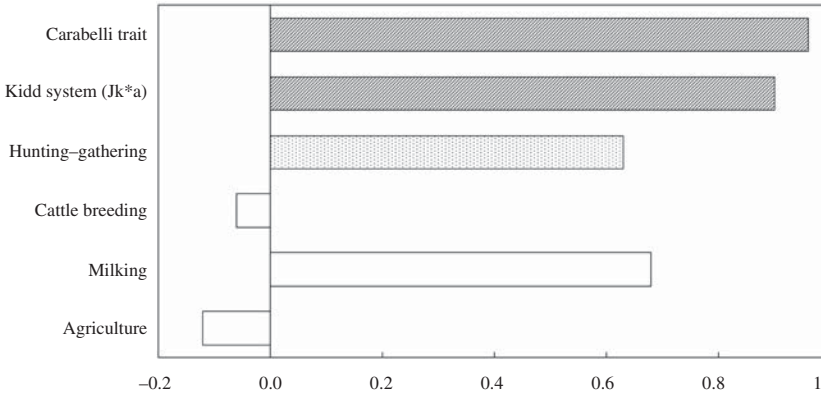

Figure 6.3. Factor loadings on the first principal component from the data set of the Carabelli trait of the maxillary first molar, allele Jk*a of the Kidd system, and the ways of life. Data source: Mizoguchi (2006).

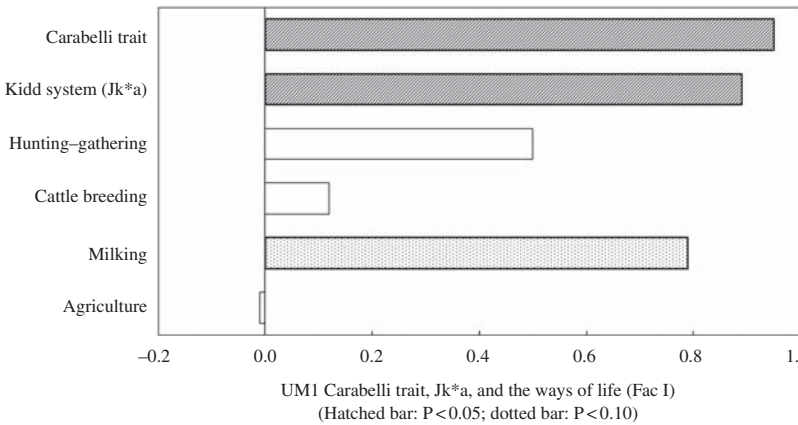

Figure 6.4. Factor loadings on the first rotated factor from the data set of the Carabelli trait of the maxillary first molar, allele Jk*a of the Kidd system, and the ways of life. Data source: Mizoguchi (2006).

as PC 1 or Fac 1 is independent of PC 2 or Fac 2, the results shown by PC 1 and Fac 1 (Figures 6.3 and 6.4) suggest that hunter-gatherers with the milking subsistence technique have relatively well-developed Carabelli's cusps and allele Jk*a at high frequencies. It has been suggested that UM1 Carabelli's trait is strongly, positively associated with milking and inversely associated with mean

relative annual humidity and annual rainfall (Mizoguchi 1993a). Therefore, although the role of allele Jk*a of the Kidd system remains to be specified in the ontogenetic process that forms Carabelli's cusp, the strong association between these characters is possibly not due to genetic drift, but rather to adaptation to shared unknown environmental factors involving milking.

6.4 The evolutionary background of morphological characters

Some researchers say that very small or faint dental characters, like mamelons along the incisal edge of anterior teeth, accessory tubercles on molar occlusal surfaces, and others, are easily worn off soon after teeth erupt. Do such characters have a function that is sufficiently significant to be impacted by natural selection? The present author feels the answer is "yes." Each dental character not only has biomechanical, behavioral, and psychological (aesthetics in humans) functions, but an ontogenetic one as well. A certain small character may function as an organizer of other tissues or substructures around it, or as a base or brace for a contiguous character in the ontogenetic process of a set of characters, or a character complex, that includes them. Such a character has no direct biomechanical function but can be a definite subject of natural selection as part of a character complex. This is one reason why the author (Mizoguchi 1994, 2006) examined dental characters relative to biochemical and physiological characters.

Ecological or among-population correlation between a character and an environmental factor is generally considered to result from one or more of three basic evolutionary causes, that is, adaptation to local environments through natural selection, random genetic drift, or gene flow (i.e., migration and/or hybridization with other populations) (e.g., Dobzhansky 1963; Harrison et al. 1977; Marks 1995; Mettler and Gregg 1969; Molnar 1992; Stern 1960). Although it is difficult to determine the precise causes for such ecological correlations, some can be explained. For example, let us assume that genetic drift occurred when a small population colonized a new region. In this case, an allele for a monogenic or oligogenic character (e.g., a particular blood-group phenotype) can change to another allele; if so, the phenotype drastically changes as a result. However, a morphological character controlled by polygenes with a minor and averaged effect may cause limited changes to the phenotype; the reason is that most migrants share substantially similar combinations of alleles across relevant polygenic sites with most members of their original population. In a case like this, it is expected that, as shown in Table 6.1, the ecological correlation between the monogenic or oligogenic character and an environmental factor such as average annual temperature may or may not be high; however, the ecological correlation between the morphological (i.e., polygenic) character and

Table 6.1. *Expected values (in absolute value) of the ecological correlation of a character with another character or an environmental factor for possible causes by thought experiment*

		Possible causes for an ecological correlation in evolutionary processes											
		Mutation			Genetic drift			Adaptation to environment through selection			Gene flow (migration/ hybridization)		
Control factors for the phenotypic expressions of two characters to be compared	Variables to be compared	Polygenic char.	Oligogenic char.	Monogenic char.	Polygenic char.	Oligogenic char.	Monogenic char.	Polygenic char.	Oligogenic char.	Monogenic char.	Polygenic char.	Oligogenic char.	Monogenic char.
Independent genes	Polygenic character	0	–	–	very low	–	–	0	–	–	high	–	–
	Oligogenic character	0	0	–	very low	not low	–	0	0	–	high	high	–
	Monogenic character	0	0	0	very low	not low	not low	0	0	0	high	high	high
	Environmental factor	very low	low	low	0 – very low	0 – high	0 – high	high	high	high	low – high	low – high	low – high
Linkage on chromosome	Polygenic character	high	–	–	low – high	–	–	0	–	–	high	–	–
	Oligogenic character	low – high	low – high	–	low – high	not low	–	0	0	–	high	high	–
	Monogenic character	low – high	low – high	low – high	low – high	not low	not low	0	0	0	high	high	high
	Environmental factor	very low	low	low	0 – very low	0 – high	0 – high	high	high	high	low – high	low – high	low – high
Pleiotropic gene(s)	Polygenic character	1	–	–	1	–	–	1	–	–	1	–	–
	Oligogenic character	–	1	–	–	1	–	–	1	–	–	1	–
	Monogenic character	–	–	1	–	–	1	–	–	1	–	–	1
	Environmental factor	very low	low	low	0 – very low	0 – high	0 – high	high	high	high	low – high	low – high	low – high

The same ontogenetic process, the same physiological cycle, etc.	Polygenic character	high	–	–	high	–	–	high	–	–	high	–	–
	Oligogenic character	low – high	low – high	–	low – high	low – high	–	high	high	–	high	high	–
	Monogenic character	low – high	low – high	low – high	low – high	low – high	low – high	high	high	high	high	high	high
	Environmental factor	very low	low	low	0 – very low	0 – high	0 – high	high	high	high	low – high	low – high	low – high
Shared high susceptibility to an environmental factor	Polygenic character	high	–	–	0 – high	–	–	high	–	–	high	–	–
	Oligogenic character	low – high	low – high	–	low – high	low – high	–	high	high	–	high	high	–
	Monogenic character	low – high	low – high	low – high	low – high	low – high	low – high	high	high	high	high	high	high
	Environmental factor	0 – high	0 – high	0 – high	0 – high	0 – high	0 – high	high	high	high	0 – high	0 – high	0 – high

Note: These expected values, which themselves may have to be further reconsidered, may be ascertained by the methods of confirmatory type based on a model, such as the restricted factor analysis of confirmatory type, path analysis, Mantel's matrix permutation procedure, etc.

the factor, or between the morphological and monogenic or oligogenic characters, is close to zero. On the other hand, if geographical variations of two or more characters, whether controlled by a major gene or polygenes, are resultant phenomena of adaptation to an environmental factor, then the ecological correlations of these characters with one another and with the environmental factor may both be high (Table 6.1).

If recent gene flow is a main cause for geographical clines in gene frequency or phenotypic value, then the directions of the clines for most characters should be consistent with one another. Also in this case, ecological correlations of the characters with one another and with some environmental factors may both be high (Table 6.1).

There are also other possible causes for ecological correlation between two characters: pleiotropic genes, linkage of genes, the state of two characters being elements in the same ontogenetic process or physiological cycle, and others. For example, Kimura et al. (2009) reported that the number of *EDAR* 1540C alleles in an individual was strongly correlated with the grade of shoveling. This does not mean that the *EDAR* gene controls the expression of shoveling. *EDAR* is also associated with several other ectodermal organs such as hair and sweat glands (Tabata 2004). Although details of the signaling pathway in which this gene functions have been elucidated to some extent, all genes relating to the expression of incisor shoveling are not yet clarified. Cohen et al. (1970) showed that the frequency of shoveling was 26.5 percent in trisomy G patients (chromosome 21) and 9.0 percent in normal controls, though the biological derivations of the samples were not described. Still, if the derivations of the patients and controls are the same, as concluded by Cohen and colleagues, then their finding suggests that some common factors influence damage to the central nervous system and tooth crown morphology of ectodermal origin. If so, a more complicated network of ontogenetic processes or physiological cycles may be associated with shoveling expression.

Table 6.1 is a list of expected values of the ecological correlation between one character and another, or with an environmental factor for possible causes obtained by a rough thought experiment. Although these expected values may be reconsidered, building and checking models of evolutionary processes on the basis of such theoretical frameworks are important to clarify the evolutionary background of morphological characters. To carry this out, the methods of a confirmatory type based on a model, such as the restricted factor analysis of confirmatory type (Jöreskog 1966; Lawley and Maxwell 1963; Mizoguchi 1980), path analysis (Kempthorne 1969; Li 1956, 1975; Mizoguchi 1978, 1986, 2010; Wright 1934; Yasuda 1969), and Mantel's matrix permutation procedure (Dietz 1983; Dow and Cheverud 1985; Dow et al. 1987; Kempthorne 1969; Mantel 1967; Mizoguchi 1993b, 2010), may be useful.

Before conducting such analyses, however, we must collect more data on modern humans and their ancestral remains. Mizoguchi (1985, 1993a, 2006) attempted to collect dental data for modern humans from various world regions. However, the data were geographically biased toward Asians. As far as the present author knows, dental data of African people are limited, though a considerable amount of nonmetric dental data of Africans have been reported by Irish (1997, present volume).

It must be stressed that the lack of paleoenvironmental data is a serious problem for clarifying the evolutionary background of morphological characters. We should intensively collect data on paleoenvironmental factors (animal bones, pollen, stable isotopes, etc.) for various regions in the world in addition to making observations on the teeth of human remains.

6.5 Summary and conclusions

Previous studies by the author on among-population associations between dental characters and environmental factors were outlined. The most recent analyses of seven dental characters, thirty-seven alleles for biochemical/physiological characters, and six climatic and four subsistence-way variables show the following: (1) MD crown diameters of UI1, UM1, and UM2 have inverse associations with allele B of the ABO system; (2) the MD crown diameter of UM1 is positively associated with haptoglobin-alpha allele 1 and average temperature in the coldest month; (3) the BL diameter of UM2 is inversely associated with alleles MS of the MNS system and positively associated with annual temperature and rainfall; (4) UI1 shoveling is positively associated with alleles cDE of the Rhesus system; and (5) the Carabelli trait is positively associated with allele Jk*a of the Kidd system and, simultaneously, tends to be associated with hunting-gathering and milking. These significant associations were considered as possible adaptations to the same environmental factors rather than a product of genetic drift.

A theoretical framework for building evolutionary models was presented to stimulate research on the evolutionary background of morphological characters. Collecting more paleoenvironmental data to complement our knowledge of patterned dental variation is of paramount importance.

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7 *Using geometric morphometrics to study the mechanisms that pattern primate dental variation*

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7.1 Introduction

In the late twentieth century, a shift in morphological analyses emerged. Rather than focusing on linear measurements and qualitative descriptions of shape, it became possible to describe quantitatively and compare morphology (Adams et al. 2004). While the dilemma of oversimplifying linear measurements had long been recognized, it was not until a new method, "geometric morphometrics" (GM), was developed that morphologists could finally analyze the shape between linear end points quantitatively (Rohlf and Marcus 1993).

The quantification and analysis of shape offered by GM can provide insight into the essential biological questions, as has been demonstrated for many skeletal phenotypes, including teeth. In this chapter we introduce various GM approaches and review ways they have been applied to studying mammalian teeth, highlighting work on primates.

One area of research receiving more and more attention is the use of morphological variation within and between populations to elucidate developmental mechanisms, and thereby inform on the evolution of these mechanisms. Teeth play an important role. As our knowledge of the genetic organization of dental development expands, opportunities for exploring the relationship between these processes and the shape of the adult dentition using GM increase.

Following this research vein, we provide a review of our current knowledge of tooth developmental genetics, with special emphasis on the hierarchical structure of the dentition. We then highlight several studies that used GM to

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test hypotheses about dental development. We present our own study of shape variation in the tooth row of *Colobus guereza* to illustrate the insights into mammalian tooth development that can be gained.

7.2 Geometric morphometric approaches

There are two approaches taken with GM: those that are landmark based and those that are not. Landmark-based studies incorporate coordinate-based (e.g., generalized Procrustes analyses, GPA) or coordinate free approaches (e.g., Euclidean distance matrix analysis, EDMA). Non-landmark-based approaches include eigenshape and Fourier analyses. In the following we review morphometric techniques most commonly applied to the study of shape in the dentition.

7.2.1 Generalized Procrustes analysis (GPA)

An important contribution to the field of morphometrics came from the technique of superimposition (Boas 1905), in which pairs of corresponding landmarks on two or more objects are directly contrasted. This method was quantified more specifically by Phelps (1932), who suggested measuring the difference between superimposed cranial forms using the Euclidean distance between landmarks, thus paving the way for future techniques like EDMA (discussed later). Sneath (1967) introduced the least-squares method of superimposition in which the landmarks of two specimens are arranged to minimize the sum of squared distances between loci. Gower (1975) generalized Sneath's pair-wise comparison for simultaneous translation, scaling, reflection, and rotation of multiple forms. Siegel and Benson (1982) followed by demonstrating that with least-squares superimposition, high variation around one or several landmarks would be distributed across the configuration, potentially obscuring shape differences between specimens. To avoid this problem, Siegel and Benson (1982) introduced a resistant-fit model, which limits the effects of regions of large variation on the fit of unchanged regions.

Today, the most widely used method of superimposition is generalized Procrustes analysis (GPA), a method of superimposition in which shapes are compared by configuring the centroid of each to an origin and scaling to a common size (Bookstein 1986; Rohlf and Slice 1990). Each shape is then rotated to a position that minimizes the squared distances between homologous landmarks (Gower 1975; Rohlf and Slice 1990).

There are some limitations to GPA. One requirement is that all landmarks be homologous and consistently identifiable across specimens (Zelditch et al.

2004). This can be limiting when studying anatomy with few such landmarks or in instances where landmarks are missing (e.g., worn teeth). A further criticism is that it cannot investigate shapes that contain presence/absence characters (Zelditch et al. 2004). Recently, however, Gómez-Robles et al. (2011) demonstrated the ability of GM techniques to investigate evolutionary novelties. Looking at two-dimensional occlusal morphologies of multiple hominid species to identify the presence (and subsequent loss) of a fifth cusp, they show that GPA is capable of discerning structures with evolutionary novelties by using sliding semilandmarks and only a single landmark associated with the novelty.

7.2.2 Euclidean distance matrix analysis (EDMA)

In 1991, Lele described an alternative method for studying group variation in two- and three-dimensional shapes. EDMA calculates Euclidean distances between all plotted landmarks on an object and compares it to a similarly landmarked object by calculating ratios of between-landmark distances in a matrix. EDMA is independent of rotation, position, and reflection of an object (Lele and Richtsmeier 1991).

EDMA, though useful in analyzing variation in shapes between groups, is not without limitations. Because EDMA techniques do not scale and use actual distances between points, an average shape will be more influenced by larger specimens (Rohlf 2000). Rohlf (2000) also describes inadequacies in the statistical power. Further, EDMA techniques are not easily visualized (see Richtsmeier et al. 2002 for discussion).

7.2.3 Eigenshape and Fourier analyses

In 1965, Lu was one of the first to recognize the ability to define curves of biological forms mathematically. He applied a harmonic analysis with three-way Fourier equations to investigate shape of the human face. A parametric approach was developed by Kuhl and Giardina (1982): elliptical Fourier analysis. Here, separate harmonics plot as ellipses and sum to the original polygonal approximation. Contemporary with the refinement of Fourier analysis was the introduction of eigenshape analysis. The latter involves comparisons of shapes of outlines of specimens by deriving a set of orthogonal shape patterns using eigenfunctions (Lohman 1983). While eigenshape chooses the optimal orthogonal function, Fourier analysis must choose from a limited number of harmonic functions (Lohman 1983).

7.3 Application of GM to studying dental variation

All of the preceding techniques have been employed in studies of dental shape variation to address a variety of biological questions. While many contributions have focused on primates, we include other mammalian groups in our review as those studies help us better understand the applicability of using GM on the primate dentition.

7.3.1 Taxonomy

Most GM work on the dentition has addressed variation in tooth shape between one or more groups; oftentimes the purpose is to distinguish taxa or identify population- or sex-specific differences in form.

7.3.1.1 Primate studies

The use of GPA to study tooth shape is dominated by work on hominoid evolution. One exception is the study of Kondo and Natori (2004), who superimposed landmarks corresponding to grooves and cusps of the occlusal surface of macaque molars to identify sex differences in shape and centroid size.

Within the hominid-focused literature, in the first of a series of papers, Martinón-Torres et al. (2006) performed a diagnostic analysis of species of *Homo* by superimposing landmarks and semilandmarks on internal crown surface features and the crown outline of LP2s. They identified a primitive-to-derived gradient from asymmetrical to more symmetrical outlines, following a general trend of dental reduction. Using the same methods, Goméz-Robles and colleagues (2007) continued by examining UM1 shape across *Homo*, distinguishing the distally displaced lingual cusps and large hypocone of Neanderthals from the relatively round external outline in modern humans. Finally, Goméz-Robles et al. (2008) compared LM1s across a sample that included *Australopithecus* and identified a trend of increased outline symmetry and talonid reduction from early to recent hominids, a result consistent with their study of the lower fourth premolar (Martinón-Torres et al. 2006).

Xing et al. (2009) applied GPA of landmarks and semilandmarks to compare mandibular premolar shape in Zhoukoudian *Homo erectus* with representatives of *Australopithecus*, African early *Homo*, Asian *Homo erectus* outside Zhoukoudian, European Pleistocene fossil hominids, and recent Chinese. They observed the preservation of several primitive hominid traits in Zhoukoudian specimens, including asymmetrical crown outlines and pronounced grooves

on the buccal side of the crown, and a high degree of disparity from European Pleistocene specimens.

Liu and colleagues (2010) assessed the taxonomy of the Pleistocene Jianshi hominids (China) by superimposing crown landmarks and semilandmarks of three Jianshi postcanine teeth with comparative fossil teeth from hominids from Europe, Africa, and Asia. Their analysis found that the degree of symmetry and cusp patterns of the Jianshi teeth resembled Asian early and middle Pleistocene hominid teeth, but not those of *Australopithecus*; the latter had a wider variation in crown shape relative to Asian hominids.

Variation in the shape of the enamel-dentine junction (EDJ) has been captured using superimposition of two-dimensional landmarks from histological sections in human lower molars (Smith et al. 2006). Skinner et al. (2008) expanded upon this technique by combining GPA with micro-CT to analyze EDJ shape differences of mandibular molars between *Australopithecus robustus* and *Australopithecus africanus*. Variation in EDJ shape, as captured by three-dimensional landmarks along the marginal ridge connecting dentine horns and along the curve of the cervix, successfully distinguished the two taxa (Skinner et al. 2008). Skinner et al. (2009) also showed that superimposition of LM1 and LM2 EDJ shapes can distinguish species and subspecies within *Pan*. The authors found significantly different shapes in dentine horn height and position, as well as dentine crown height and crown base shape, between *P. paniscus* and *P. troglodytes* and between the subspecies *P. t. troglodytes* and *P. t. versus*.

EDMA has also been successfully employed in studies of dental variation across different primate species. In analyzing the dental morphology of extant *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes*, and 19 Sterkfontein Member 4 hominid molars, Hlusko (2002) collected cross-sectional and occlusal landmarks and analyzed Euclidean distances between them. She found significant cross-sectional shape differences between first and second molars. It was concluded that metameric variation can provide functional and developmental information previously unattainable from fossils and from tooth shape more generally.

Olejniczak et al. (2004) investigated evolutionary relationships between extant primates by analyzing Euclidean distances between nine landmarks on the EDJs of maxillary molars. They demonstrated the ability of dentine shape to deduce the relationships among hominoid, cercopithecoid, and ceboid primates accurately. Additionally, EDMA has been used to support the close relationship of late Miocene hominoids and orangutans; Liu et al. (2001) analyzed seven landmarks on three molars, showing that cross sections of specimens from Yuanmou, China, are more similar to those of great apes than of humans. Further, they demonstrated strong affinities between the late Miocene hominoids, *Lufengpithecus lufengensis*, *Sivapithecus*, and the Yuanmou specimens.

EDMA has also been used to study morphological variation in other aspects of dental form, such as dental arch variation. Ferrario et al. (1993a, 1993b, 1994) calculated Euclidean distances between seven landmarks on each hemirow of the mandibular and maxillary tooth rows to assess asymmetry and shape dimorphism between men and women.

Landmark-free techniques have also been used to study hominid dental morphology. Examining LP2s between Neanderthals and modern humans, Bailey and Lynch (2005) applied elliptical Fourier analysis to show that Neanderthal cheek teeth have truncated mesiolingual lobes, producing asymmetrical teeth. This character state was found to be derived and the symmetrical LP2s in modern humans were found to be primitive.

7.3.1.2 Nonprimate studies

Compared to the fairly straightforward taxon diagnoses exemplified by the preceding work, larger sample sizes for nonprimate taxa, particularly for fossil assemblages, enable researchers to ask more complex questions about species relationships. Differentiation between taxonomic groups based on dental landmark data is particularly prevalent in the study of extant and fossil rodents. Van Dam (1996) demonstrated the utility of GM tooth shape analysis for classification of fossil murids. The author collected landmark data to quantify the degree of stephanodonty, a complex, ridged crown structure, in the UM1. A comparable approach was used by Janžekovič and Kryštufek to separate species of rock mice of the genus *Apodemus* on the basis of the shape of the upper molar row (Janžekovič and Kryštufek 2004; Kryštufek and Janžekovič 2005). Similarly, Wallace (2006) used LM1 shape to differentiate between two species of the vole *Microtus*. Macholán (2006) used a combination of landmarks and sliding semilandmarks to capture shape variation in the outline of the UM1 of extant and extinct members of the genus *Mus*.

Pavlinov and colleagues have used landmark-based analyses to classify a variety of taxa. Their earliest work explored occlusal shape variation in the UM3s of subspecies of the vole *Alticola argentatus* (Pavlinov et al. 1994; Pavlinov 1999). Pavlinov (2001) compared UM1 shape across seven genera from the rodent family Gliridae followed by studies on upper tooth row shape in eight species of brown-toothed shrews of the genus *Sorex* (Pavlinov 2004a, 2004b) and upper postcanine tooth row shape among island and mainland populations of the Eurasian polar fox, *Alopex lagopus* (Pavlinov and Nanova 2008).

Polly and colleagues have utilized landmarks to quantify variation in tooth shape in the context of paleophylogeography and dating of species divergences. Polly (2001, 2003b) reconstructed phylogeographic relationships between fossil and modern samples of the European shrew *Sorex araneus* using lower

first molar shape. Polly (2002) also examined the relationship between the amount of LM1 shape divergence and the amount of divergence time separating Paleogene viverrid carnivoran populations. More recently, Polly and colleagues (2005) used landmarks to assess the degree of occlusal fit between UM1s and LM1s in sixteen species of bats.

Marcolini and colleagues have shown that landmark-based and Fourier outline analyses of tooth shape can be taxonomically informative in rodents. They examined LM1 occlusal surface and enamel-dentine junction shape in a fossil vole, *Ogmodontomys*, using landmarks and semilandmarks (Marcolini et al. 2009). Marcolini (2006) used Fourier analysis to decompose LM1 contours of six species of extinct *Mimomys* from the Pliocene and Pleistocene.

Hurth et al. (2003) distinguished six separate Plio-Pleistocene *Mimomys* species also on the basis of Fourier data from the LM1. Other explorations of systematics in the fossil record using Fourier methods include Renaud and colleagues' (1996, 1999b) study of UM1 shape in Pliocene lineages of the rodent *Stephanomys* and Miocene murines, as well as Angelone's (2008) study of the LP1 of *Prolagus*, a fossil lagomorph. Leroy et al. (2004) developed criteria for classifying fossil shrews based on Fourier analysis of UM1-UM2 and LM1-LM2 as well as the UP2 of three extant species of the genus *Crocidura*.

Cucchi and colleagues (2009, 2011) have studied the taxonomic significance of the shape of pig mandibular molars in island Southeast Asia and China. Fourier analysis of the outline of the LM3 was used to investigate the history of pig domestication on the basis of Holocene *Sus* remains from Malaysia (Cucchi et al. 2009). Occlusal cusp landmarks and outline semilandmarks of the LM3 were used in a separate study on Neolithic and modern pigs from China (Cucchi et al. 2011). Cucchi (2008) also implemented Fourier analysis in the taxonomic identification of a house mouse LM1 associated with a Late Bronze Age Mediterranean shipwreck. Additionally, house mouse lower molar shape has been contrasted in Canary Island and continental populations using Fourier analysis (Michaux et al. 2007).

Molar outline shape can also be quantified using eigenshape analysis, as demonstrated by Polly's (2003a) study of living and fossil marmots. The author used shape divergence in the outline of LM3s to reconstruct phylogenetic relationships among more than a dozen subspecies of the genus *Marmota*.

7.3.2 Ecology and adaptation

The potential for drawing connections between tooth shape and environmental factors, specifically diet, using GM has been well-demonstrated across vertebrates generally, but it has not been widely employed to study dental adaptation

in primates. In one of the only primate adaptation studies, White (2009) collected landmarks corresponding to the cusps of lower molars in modern lemurs, lorises, and tarsiers to contrast tooth shape across a range of dietary strategies. Frugivorous and graminivorous taxa were distinguished from folivores and insectivores on the basis of relative cusp orientation, with omnivores being intermediate between these three groups.

The evolution of tooth shape with regard to selection by environmental factors in nonprimates has been studied extensively using landmark- and outline-based methods. Polly (2004) performed stochastic computer simulations of four different evolutionary modes for UM1 shape in the shrew *Sorex araneus*, including randomly fluctuating selection, directional selection, stabilizing selection, and genetic drift. Comparison with real shrew molar landmark data identified randomly fluctuating selection as the predominant mode. Wood and colleagues (2007) addressed evolutionary stasis in the dentition of the condylarth *Ectocion* over changing environmental conditions in the Paleocene-Eocene. They collected occlusal surface landmarks and outline semilandmarks for the LP2, LM1, and LM3 and tested variation in tooth shape over time against a null model of a random walk.

Rychlik and colleagues (2006) used a landmark approach to study the effects of sympatry on the shape of the cranium, mandible, and UM1 of two species of Polish water shrew (genus *Neomys*). Partial least squares (PLS) analysis of shape and geoclimatic data showed similar ecophenotypic responses for the two species when sharing the same environment. Piras et al. (2009) used the $\delta^{18}O$ isotope record as a proxy for climate in their study of the relationship between environment and LM1 shape in extinct populations of the vole *Terricola savii*. A temporal trend correlated with $\delta^{18}O$ was detected in univariate analyses of shape based on a combination of landmarks and semilandmarks. An analysis of LM1 shape in extant populations of *T. savii* revealed a similar relationship (Piras et al. 2010). McGuire (2010) addressed the relationship between climate and LM1 shape in the vole *Microtus californicus*. Shape variation drawn from landmarks on the molar occlusal outline was analyzed in the context of geography using PLS. A gradient of shape difference between northwest and southeast California populations was identified, revealing a significant climate signal.

Caumul and Polly (2005) investigated the relationship between environmental factors and cranium, mandible, and LM3 shape in Eurasian marmots. After capturing molar outline shape using semilandmarks, the authors used path analysis to determine the percentage of shape variation explained by the effects of diet, habitat, elevation, temperature, precipitation, body size, and mitochondrial deoxyribonucleic acid (mtDNA) genetic divergence. Stynder (2009) also used landmark and semilandmark data from multiple teeth to study niche

partitioning among fossil hyenas. Comparison of the outlines of the crowns of the LP1, LP2, and LM1 suggested differences in the degree of carnivory among four late Miocene/early Pliocene species.

Ledevin and colleagues (2010a) analyzed variation in the occlusal outline of UM1, UM3, and LM1s of Quaternary European lineages of the bank vole (*Myodes*) using Fourier analysis. A subsequent Fourier analysis of the UM3 identified season of trapping and related wear patterns as a source of shape variation of the same order of magnitude as biogeographic variation (Guéréchau et al. 2010). A third study of UM3 outline in *Myodes* identified another source of variation secondary to trapping season and wear: the presence or absence of a fourth lingual triangle (Ledevin et al. 2010b). The authors attributed this variation to the space available to the molar at the posterior end of the row, suggesting an epigenetic factor, such as maternal health, as the source.

Renaud and colleagues implemented Fourier analysis of molar outline to explore the relationship between tooth shape and a wide range of ecological factors, including geography, diet, climate, habitat and age. Renaud (1999) began by examining UM1 and LM1 outline shape across the geographic range of the African murine rodent *Oenomys*. Next, the authors studied these same teeth in the Miocene murine *Paraethomys* with respect to the climatic record (Renaud et al. 1999a). Renaud and van Dam (2002) also examined Miocene murine molar outline variation, concentrating on morphological evolution associated with a dietary shift from granivory to herbivory. Renaud and colleagues then drew upon this work to characterize the diet of the extinct lava mouse *Malpaisomys* from the Canary Islands (Renaud and Michaux 2004) and later of an entire lineage of rodents spanning a nine-million-year interval in the Neogene (Renaud et al. 2005). More recently they looked at the effects of sex and age (Renaud 2005), as well as adaptation to insular conditions, in the UM1 outline of island and mainland *Apodemus sylvaticus* wood mice (Renaud and Michaux 2007).

7.3.3 Pathology and forensics

GM has also been applied to investigations of asymmetry and malocclusion in the human dentition. Schaefer et al. (2005) investigated dental arch asymmetry in a modern inbred population from an isolated island in the Adriatic Sea. They plotted landmarks along the buccal surface of mandibular and maxillary teeth and compared shapes with a more heterogeneous population in mainland Croatia. Fluctuating asymmetry (FA, asymmetry between either side of the midline) was higher in the inbred population, suggesting genetic and environmental factors play a part in the asymmetry of these populations.

Nie and Lin (2006) compared dental arch forms between normal occlusion and Class II Division 1 malocclusion groups by performing EDMA on distances between landmarks along the maxillary and mandibular arches. Banabilh et al. (2008) used GPA to compare arch morphologies in Asian adults with obstructive sleep apnea (OSA) with unaffected Asian adults. They compared landmarks on cusps and incisor edges and found that maxillary arches in adults with OSA were narrower in the transverse plane of the incisor and canine region; they also found that mandibular arches in people with OSA were narrower in the anterior-posterior plane of the premolar and molar regions.

It is worthwhile to note the GM contributions to bite mark identification in forensic analyses. Kieser et al. (2007) analyzed bite marks of 50 orthodontics casts to determine their uniqueness. By plotting landmarks and semilandmarks, they show the incisal surfaces of the mandibular and maxillary dentitions are unique. Bush and colleagues (2011) examined human bite marks on cadavers and anterior dentition casts to determine whether these pieces of evidence were reliable in identifying a particular dentition. Using incisal surface landmarks in two-dimensional scans of bite marks, they analyzed variation caused by an experimental biting of skin. They show that skin distortion resulted in several distinct patterns and suggest using caution when attempting individual identification. In the context of fossil assemblages, Benazzi and colleagues (2011) assessed the use of Fourier analysis on interproximal wear facet shape to identify and match isolated tooth crowns; however, they concluded that this approach should only be used with other analyses to determine the minimum number of individuals.

7.4 Tooth development

In addition to questions of taxonomy, ecology, pathology, and forensics, dental researchers are increasingly motivated to understand how teeth develop as structures, linking phenotypic variation to the developmental processes that underlie it. As teeth vary in shape in many dimensions (e.g., tooth type, occlusal surface, cross section, wear pattern) and on several hierarchical levels (e.g., shape of individual tooth, collective shape of all teeth belonging to a single type, or shape of entire tooth row), GM can be valuable for quantifying phenotypic variation at these scales and consequently help elucidate underling developmental mechanisms.

Most of what is known about the genetic mechanisms specifying and patterning the dentition is known from laboratory mouse and chicken models. Although the mouse dentition is relatively specialized (and reduced) compared to most mammals (Figure 7.1), we focus on the mouse model as it presents the

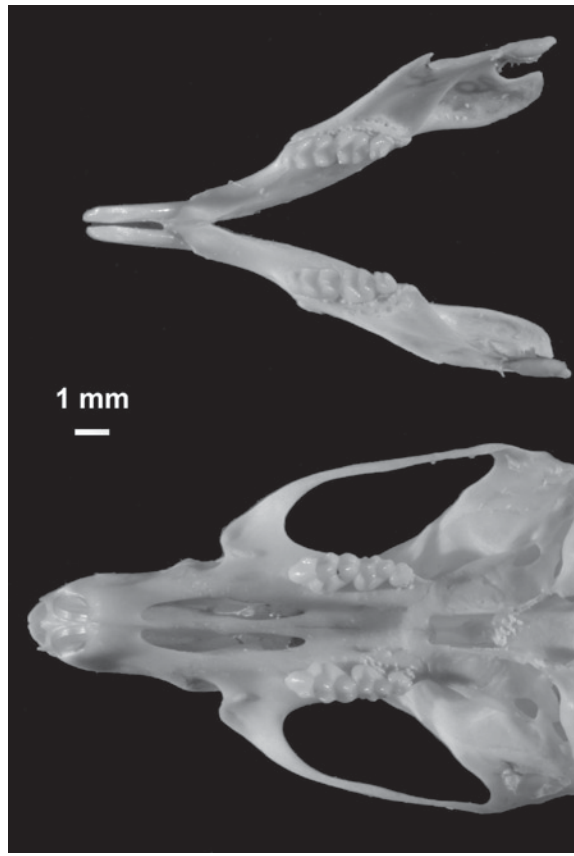

Figure 7.1. Mouse maxillary and mandibular dentitions. Note the highly derived and reduced dental formula of one incisor and three molars.

most complete picture of development and is referred to for human odontogenesis (e.g., McCollum and Sharpe 2001).

The overview of tooth and early craniofacial development that follows is focused on setting up hypotheses that can be tested through GM. For additional overviews of odontogenesis we refer the reader to Michon (2011), Cobourne and Sharpe (2010), Simmer et al. (2010), Lesot and Brook (2009), Mitsiadis and Graf (2009), and Salazar-Ciudad (2008).

7.4.1 From stomodeum to cap stage

Consideration of mouse tooth development needs to begin at least 4 embryonic days prior to any histological evidence of teeth; cell fate this early on appears

to influence later odontogenic potential. The stomodeum, or embryonic mouth, forms where head surface ectoderm and gut endoderm meet. Between E8.5 (the 8.5th mouse embryonic day *in utero*) and E9.5, cell death at this interface connects the feeding opening to the developing digestive tract (Poelmann et al. 1985). Sonic hedgehog in the pharyngeal endoderm induces *Fgf8* in what will become the mouth epithelium, with *Bmp4* expressed and acting as an inhibitor in the adjacent, non-mouth ectoderm (Haworth et al. 2004, 2007; Shigetani et al. 2000). These *Fgf8* and *Bmp4* expression domains are then maintained by *Pitx2* in the stomodeal ectoderm throughout early mouth patterning (Liu et al. 2003; Ohazama et al. 2010). Their expression is essential for the maintenance of downstream gene expression in assembling dental arch mesenchyme and determining oral/aboral and dorsoventral patterning.

Anterior-posterior patterning in the dental arches comes from migrating streams of neural crest mesenchyme, which leave the developing brain and form pharyngeal arches at E8.5–E9.75 (Serbedzija et al. 1992). These arches are serially homologous primordia arranged rostrocaudally that give rise to the jaws and throat structures (recently reviewed in Graham 2008; Kulesa et al. 2010). The identity of these arches is somewhat influenced before migration by the nested expression of *Hox* genes along the body axis (Minoux and Rijli 2010).

In the early embryo, mesiodistal polarity within each arch arises from dorsoventral patterning of the pharyngeal arches. During E8.25–E9, endothelin-1 from the endoderm activates nested patterns of *Dlx* genes along the dorsoventral axis of the pharyngeal arch mesenchyme via a hypothesized signaling gradient (Benouaiche et al. 2008; Creuzet et al. 2005; reviewed in Minoux and Rijli 2010). The mandibular prominences are distinguished molecularly from the maxillary prominences by a *Dlx5/6*-driven developmental program and receipt of the endothelin-1 signal (Sato et al. 2008). Other genes are differentially expressed in the maxilla and mandible as a result of differential *Dlx* expression (Minoux and Rijli 2010). The frontonasal mass neural crest, which also contributes to the premaxillary and maxillary incisor region, is less well characterized.

At mouse E10 and E10.5, the early broad expression of transcription factors and signaling molecules becomes more localized within the oral epithelium and mesenchyme. By E11, a primary epithelial band forms, a stripe of slightly thickened epithelium along both maxillary and mandibular arches, from which the dental lamina arises (Jernvall and Thesleff 2000; Nanci 2008). This dental lamina region expresses *Shh* and *Pitx2* (Keränen et al. 1999), a restriction of the former stomodeal expression domains of these molecules (Mucchielli et al. 1997).

The physical creation of individual teeth from epithelial and mesenchymal tissue layers occurs through the process of morphogenesis. There is a developmental shift from an instructive epithelium (Lumsden 1988) to instructive

mesenchyme around E11.5, after which genes expressed in the developing dental mesenchyme and papilla direct tooth morphogenesis (Kollar and Baird 1969, 1970; Mina and Kollar 1987). We present the major events of tooth morphogenesis through the cap stage only.

The first morphological signs of individual tooth morphogenesis have been reported as early as mouse E10.5, with the thickening of the dental epithelium in foci (Kratochwil et al. 1996; Mucchieli et al. 1997). Each thickening, called a tooth placode, is hypothesized to be induced by epithelium-induced *Bmp4* and *ActivinβA* in the mesenchyme (Jernvall and Thesleff 2000), with a half-day delay between molars and incisors (Ruch 1984). Most studies show that localized mesenchymal gene expression has begun under these thickenings by E11.5 (Bitgood and McMahon 1995; Ferguson et al. 1998; Vainio et al. 1993), at which time the placode itself appears to be acting as a signaling center for members of the *FGF*, *BMP*, *Shh*, and *Wnt* families to begin the transition to mesenchymal control over tooth morphogenesis (Jernvall and Thesleff 2000).

The transition from placode to bud stage (around E12.5) is one of degree, where continued proliferation of the epithelium into the underlying mesenchyme creates a mass of epithelial cells intruding into the condensing mesenchyme. *Shh* expression in the epithelium is required for proper cell proliferation (Cobourne et al. 2001; Dassule et al. 2000; Hardcastle et al. 1998), while *FGF*, *BMP*, and *Wnt* ligands expressed there are orchestrating the reciprocal epithelial-mesenchymal interactions (Chen et al. 2009; Neubüser et al. 1997; Zhang et al. 2000). By late bud stage (around E13.5), the primary enamel knot is morphologically visible (see later discussion).

Cap stage marks the beginning of crown shape morphogenesis as the epithelium encircles the mesenchymally derived dental papilla. Histologically, cap stage is diagnosed by formation of the inner and outer dental enamel epithelia, with lingual and labial sides of the inner dental epithelium separated by the enamel knot. The enamel knot is a collection of nonproliferative cells acting as a signaling center for crown formation (Jernvall et al. 1994; Vaahtokari 1996). It expresses *FGFs* to direct proliferation of epithelial cells and growth of the dental papilla, *BMPs* to maintain nonproliferation in the enamel knot, as well as *Shh*, *Wnts*, and members of several other signaling pathway families (Jernvall et al. 1998; Jernvall and Thesleff 2000; Kettunen and Thesleff 1998; Thesleff et al. 2001). Enamel knots disappear by apoptosis mediated by *Bmp4* and *jagged 2*, a Notch family ligand (Jernvall et al. 1998; Mitsiadis et al. 2010). Cap stage also marks the beginning of cellular differentiation in the tooth germ.

Shh function appears to be independent of many of the other signaling pathway genes in epithelial-mesenchymal interactions, in the enamel knot, and in later morphogenesis, but it is essential for proper growth of the lingual

epithelium, for the dental cord connecting a tooth germ to oral epithelium, and for overall tooth size (Dassule et al. 2000). *Pitx2* is also critical for epithelial morphogenesis at these stages, affecting aspects of tooth orientation and/or downgrowth in the jaw, as well as cap formation (Liu et al. 2003).

The dental papilla is crucial for creating tooth shape because it is a substrate for the epithelium to fold and proliferate around and because it can induce enamel knots, apparently quite late into development (E17 in mouse transplant experiments; Kollar and Baird 1970). It is the enamel knot that seems to direct epithelial folding and proliferation to create crown shape (Jernvall et al. 1998, 2000), and the induction of primary enamel knots and, importantly, secondary enamel knots in multicusped tooth types, is dependent on signals from the papilla. Secondary enamel knots express a subset of the same genes as primary enamel knots, but the domains of these genes are less restricted; some like *Shh* and *Fgf9* connect secondary enamel knots (Dassule et al. 2000; Kettunen and Thesleff 1998). The fate of primary enamel knot cells in relation to secondary enamel knots is currently under debate, depending on what markers are used (Cho et al. 2007; Coin et al. 1999; Jernvall et al. 2000; Lesot and Brook 2009; Matalová et al. 2005; Peterková et al. 2002; Shigemura et al. 1999).

Primary enamel knots sit at the cusp tips of singly cusped teeth and form the crown base in multicusped teeth in all mammals examined (Järvinen et al. 2008; Jernvall et al. 1998, 2000; Moustakas et al. 2011; Torres et al. 2008; Yamanaka et al. 2010). Secondary enamel knots form cusp tips in molars and prefigure species-specific molar morphologies (voles: Jernvall et al. 2000; Keränen et al. 1998; possum: Moustakas et al. 2011).

7.4.2 Patterning the dental arcade

There is a fair amount of imprecision in the developmental genetics literature regarding what is called a developing individual tooth compared to an odontogenic field; however, it is clear that the potential odontogenic areas of the dental arch set up the arrangement of individual tooth primordia, creating the mammalian dental formula. We will provide an overview of what is understood about the four critical steps in patterning the mammalian (and primate) dentition: (1) the location and size of the dental lamina, (2) the specific location of dental placodes along the lamina, (3) the identity of the tooth (i.e., incisor or molar), and (4) variation within a tooth class (i.e., variation between first, second, and third molars).

Most mammals have only one row of teeth around the dental arcade, a different situation than in other vertebrates such as cichlid fish (Fraser et al. 2008). In the mouse, expression of *Wnt7* in the nondental epithelium is thought to play

a role in restricting *Shh* expression to tooth-forming sites (Sarkar et al. 2000). Zhang and colleagues (2009) found that *Osr2*, an inhibitor of mesenchymal *Bmp4* expression, is required to pattern teeth into a single tooth row in mice.

Individual tooth placode initiation along the dental lamina is an area of active research and involves a feedback mechanism of *Wnt* and *Shh* signaling (Ahn et al. 2010; Cho et al. 2011; Järvinen et al. 2006; Liu et al. 2008). This has been modeled as a reaction-diffusion process for embryonic alligator teeth (Kulesa et al. 1996) and mouse molars (Cho et al. 2011) and is similar to that invoked for feather patterning (Jiang et al. 1999, 2004) and hair follicle initiation (Sick et al. 2006). Phenotypes produced by manipulations of the candidate pathways at this point in development, however, are more complex than changes in tooth placode size, number, or spacing; this outcome may reflect later roles for these genes or the existence of other mechanistic effects of these candidate genes.

In a heterodont dentition, tooth type varies along the arcade, a fate developmentally encoded in mesenchymal cells prior to morphogenesis (prior to mouse E11). There are currently two ideas for how tooth type is determined, or, rather, how tooth shapes are patterned along the arcade. These ideas are not mutually exclusive although we describe them individually. The first is the Homeobox Code Hypothesis and the second involves specification of odontogenic fields.

The Homeobox Code Hypothesis (Sharpe 1995; Thomas and Sharpe 1998) can be viewed as a culmination of the many patterning processes prior to the dental lamina stage. It describes a group of transcription factors regionalized in partially overlapping domains in the mouse oral mesenchyme, which play a role in determining tooth type (incisors vs. molars). Genes invoked in the Homeobox Code Hypothesis are expressed long before physical signs of tooth development, and the effects of these genes on tooth type may not play out until later.

Evidence supporting this hypothesis comes from the transcription factor *Barx1*, which is normally expressed in the proximal oral mesenchyme. When *Barx1* is experimentally misexpressed in presumptive incisor regions at E10, teeth that ultimately develop are molariform (Tucker et al. 1998). Miletich et al. (2005) hypothesize that *Barx1* is responsible for activating a morphogenetic pathway instructing mesenchyme to form multicuspid teeth. Recently, Munne et al. (2010) challenged this interpretation, arguing that the *Barx1*-molariform tooth may be a fusion of small incisor-like teeth created by the breakup of enlarged mouse incisor placodes into multiple closely spaced placodes.

Barx1 expression is, however, inactivated in the maxillary molars with the double knockout of *Dlx1* and *Dlx2*, two dorsoventral patterning genes central to the Homeobox Code Hypothesis (Thomas et al. 1997; see earlier discussion). In these double knockouts, maxillary molars arrest before bud stage

(Section 7.4.1), as a result of regional misspecification of odontogenic mesenchyme as chondrogenic mesenchyme (Qiu et al. 1997; Thomas et al. 1997). As these experiments demonstrate, there are tooth type-specific defects involving the interaction of molar specification and dental arch patterning pathways, more minor adjustments of which could result in modular tooth type-related variation.

The second idea for how the tooth row is patterned concerns specification of odontogenic fields. The subsequent initiation of tooth primordia may take place where dental lamina intersects with fields of molecular signaling (Jernvall and Thesleff 2000). One hypothesis for how this field specification occurs is that morphogenesis of the embryonic jaw due to cell proliferation shifts and expands distinct epithelial domains of *Fgf8* and *Bmp4*. Opposing spatial signals from these two molecules around E10–E10.5 create patches of more localized mesenchymal gene expression, as occurs with *Pax9* (Neubüser et al. 1997). The result of these newly restricted expression patterns is the specification of incisor and molar fields, one of each per jaw quadrant (in mice), which distinguish regions of the dental arch able to form teeth from those that have lost the ability and will become other oral structures.

There is a developmental delay in specification of mandibular incisor and molar fields, with incisor fields specified only after a subtle shift in the inhibitory *Bmp4* expression pattern coupled to changes in shape and size of the developing jaw (Neubüser *et al.* 1997; Ruch 1984). Because of the changes during this delay, incisor and molar fields may acquire slightly different characteristics. There may also be intrinsic differences between maxillary incisor and molar fields; incisor fields are specified partly on the nasal processes, derived mostly from the frontonasal mass, whereas molars are specified entirely on the maxillary processes (Kriangkrai et al. 2006a 2006b; Peterková et al. 1993; Yamanaka et al. 2007; Yamanaka and Uemura 2010). The incisor field also includes lip furrow primordia (Dassule et al. 2000; Kollar and Baird 1970).

Both developmental models for tooth type specification propose hypotheses based on empirical developmental genetics for at least two tooth developmental modules: incisors and molars. Given that GM enables exploration of various combinations of landmarks, the dental phenotype can be defined in multiple ways. As such, methods for identifying which landmark combinations most accurately reflect such developmental modules can be provided and enable researchers to determine how pervasive such a pattern of phenotypic variation is across mammals and other vertebrates.

Turning to variation within a tooth class, developmental genetics studies have been restricted to the molars, because of the reduced rodent dental formula. From studies of third molar development in mice, it is clear that the odontogenic fields specified at early stages only specify the first molar and

the more mesial teeth (Chlastaková et al. 2011). The second and third molars bud off the molars mesial to them, and their size, and possible constraint on shape, is highly determined by the balance of activating and inhibiting signals received from the mesial tooth (Catón and Tucker 2009; Grewal 1962; Grüneberg 1965; Kavanagh et al. 2007).

The limited number of genetics studies of animals with premolars indicate that molars in these animals form from a posterior budding of the dental lamina; it has been suggested that they arise from a premolar field specified at homologous stages to those set up in mice and not from a distinct molar field (citations). (Järvinen et al. 2009; Yamanaka et al. 2007; Yamanaka and Uemura 2010). There is a time delay in the development of these more distal molars, as well as a different jaw ossification environment, which may also contribute to differences in these molars.

In summary, both of the current ideas for how the tooth type is patterned suggest that incisors may have some degree of developmental distinction from the molars. The embryological events observed in animals with premolars suggest there may be overlap in mechanisms underlying premolars and molars. We will now explore evidence from experimental developmental genetics for such developmental modules.

7.4.3 Evidence for molar and incisor developmental modules

The existence of tooth type-specific knockouts early in development suggests that mouse tooth type (incisor vs. molar) is already set prior to any morphological signs of tooth development. While there are numerous lines of evidence from development for distinct molar and incisor modules in mice, we will highlight four.

In *Lhx6/7* double mutants, molar teeth arrest before any sign of morphogenesis, resulting in the elimination of an entire tooth class by early mesenchymal patterning genes (Denaxa et al. 2009). Most of the localized markers for epithelial-mesenchymal interaction are unaffected, and incisor morphogenesis is normal (Denaxa et al. 2009). The authors interpret these results as a failure of molar placode specification, although many of the known inductive interactions seem to be occurring.

Activin βA is a mesenchymally expressed signaling factor, just under molar and incisor fields and induced by *Fgf8* (Ferguson et al. 1998). Knockout mice arrest at bud stage, but maxillary molars are unaffected because no signaling occurs there from activin βA or any other TGFβ molecule (Ferguson et al. 2000). Activin βA is critical for signaling back to the epithelium by E11.5 for the later bud stage to cap stage progression in all teeth but the maxillary molars (Ferguson et al. 1998). These results suggest that something intrinsic to the

maxillary molar epithelium or mesenchyme by E11.5 is different from other teeth, though that difference has not been identified.

In *Dlx1/2* knockout mutants, E11.5 maxillary molars form epithelial thickenings but do not progress beyond that stage like other teeth (Thomas et al. 1997). The combined loss of these early patterning genes prevents the action of proliferative signals between the epithelium and mesenchyme of any of the maxillary molars, reinforcing the idea that early mesenchymal expression domains can constrain later tooth developmental mechanisms in a tooth-specific fashion.

Recent reevaluation of gene expression also identified several genes previously thought to be exclusively endodermal; however, they are now known to be expressed in the early proximal mesenchyme and are proposed to influence molar tooth fate (Ohazama et al. 2010; Shigetani et al. 2000; Thomas et al. 2000).

7.4.4 Evidence for molar and premolar developmental modules

Careful histological observations have detected rudimentary tooth buds in the maxilla and mandible of mice and voles that may provide information about development of premolars (Keränen et al. 1999; Peterková et al. 2002; Prochazka et al. 2010). Most of these rudimentary tooth buds regress by apoptosis, but the LM1 in mice (but not voles) absorbs one of these rudiments onto the anterior portion of the tooth (Peterková et al. 2002; Prochazka et al. 2010; Witter et al. 2006). *Spry* mutants (and others, reviewed in D'Souza and Klein 2007) maintain these rudiments, which have been said to resemble ancestral premolars (Kangas et al. 2004; Peterková et al. 2005, 2006; Prochazka et al. 2010). It is currently unclear how mechanisms involved in the formation and regression of such tooth buds might apply to mammals lacking a diastema and possessing more tooth types. In a later section we show how GM analyses of tooth row shape variation suggest that the Old World monkey *Colobus guereza* appears to reflect an incisor versus postcanine field, and within the postcanine field a premolar and molar field.

7.4.5 Evidence for mechanisms that cause variation within a tooth class (molars)

While each individual tooth is relatively independently controlled in terms of morphogenesis by its own signaling center (Jernvall and Thesleff 2000), genes controlling morphogenesis are shared across all teeth; thus, changes in the way they function may produce shape phenotypes in all teeth in the tooth row, or all teeth within a particular tooth class.

Ectodysplasin signaling is a key feature of enamel knot formation and maintenance during crown formation (Laurikkala et al. 2001; Pispa et al. 1999; Tucker et al. 2000, 2004). While much remains to be understood about this pathway (Charles et al. 2009a), there are dosage-dependent and X-inactivation-related effects on cusp lateral spacing in mutants of this pathway, as well as effects on tooth size (Charles et al. 2009a; Grüneberg 1966; Kangas et al. 2004; Kristenová et al. 2002). Small regulatory changes in genes such as ectodysplasin could create dental polymorphism within species and explain the evolution of a wide variety of tooth morphologies among mammals, including cusp reduction and the presence of longitudinal lophs (Kangas et al. 2004).

Ectodin (*Sostdc1*) mutants form longitudinal lophs on the buccal sides of cheek teeth, caused by a reduction in intercusp regions of the crown (Kassai et al. 2005). Decreasing *Fgf3* dosage in the primary enamel knot and mesenchyme increases cusp fusion and longitudinal lophs that resemble the morphological evolution in rodents from primitive fossil forms such as *Democricetodon* and the stem murine *Potwarmus* (Charles et al. 2009b). These authors also found that molar teeth in humans deficient in *Fgf3* are missing hypocones and have only three cusps, a morphology that resembles *Bahinia*, a primitive anthropoid primate from Asia; it is possible that *Fgf3* levels may play a role in repeated evolution of the hypocone across mammals.

More generally, morphodynamic models for crown formation were proposed that link gene expression and signaling of enamel knots to cell proliferation in the developing germ and physical and mechanical constraints of the developing enamel organ. Computational models with these parameters have shown the ability to replicate cusp morphologies of a wide variety of mammalian molars (Jernvall 2000; Osborn 2008; Salazar-Ciudad and Jernvall 2002, 2010).

Several genes have been identified that influence cusp height. Downregulating *Wnt* or *Bmp4* at this stage results in flattened molar cusps, due to reduction of *Bmp4*-directed *p21* expression in secondary enamel knots (Liu et al. 2008; Tabata et al. 2002). *Wnt* knockout mice have expanded ectodin expression, but reducing ectodin expression also results in broad, flat molars (Kassai et al. 2005; Liu et al. 2008). Follistatin knockout mice, which have elevated levels of *TGFβ*-family signaling, display blunted molar cusps that are not angled mesially because of a failure of asymmetric cell proliferation in each cusp (Wang et al. 2004). Additionally, in the possum *Monodelphis domestica*, teeth with tall, sharp cusps (the canine, premolars, and molars) express *Fgf10* in their primary enamel knots, whereas in lower-cusped teeth like incisors and all mouse teeth *Fgf10* is limited to the mesenchyme (Moustakas et al. 2011).

Pitx1 knockout mice have mandible-specific cusp anomalies. There is a single cusp on the LM1 that is shorter in length than the maxillary molars

(Mitsiadis et al. 2008). There is also an incompletely penetrant LM1-LM2 fusion, hypothesized to be a result of a LM2 developmental delay. While upper and lower teeth are often differentially affected in knockout mice, this is the only example in which only the mandible is affected at this late developmental stage. Although the mechanisms behind these defects are not well understood, apoptosis and proliferation seemed normal, but *Barx1* was somewhat down-regulated in the mandibular molar mesenchyme (Mitsiadis et al. 2008).

These studies, combined with the observations of molar development, suggest that variation in the molar row may be patterned by mechanisms specific to molars, and as such the molar series in and of itself is a cohesive phenotype, as opposed to just three separate teeth. Quantitative genetic analyses of baboon dental variation provide additional evidence to the same (Hlusko et al. 2004).

7.5 GM studies on tooth development

Researchers have utilized GM to study development of the dentition in several contexts, including use of superimposition to measure phenotypes from perturbations of development at the genetic level. Most research has taken a more indirect approach, using GM data to test models of development patterning or to explore developmental constraint and modularity, on the basis of the developmental genetic literature. Primate and nonprimate work are discussed here.

7.5.1 Developmental genetics

Keller and colleagues (2007a, 2007b, 2008) examined the effects of *in utero* exposure to the toxicant 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (TCDD) on development of the murine mandibular molar row. Landmarks from left and right molars were used to assess fluctuating asymmetry in control and TCDD-exposed mice. Genotypic effects were identified in a mixed-model ANOVA of shape variation, but a subsequent quantitative trait locus (QTL) analysis did not reveal any different gene action between groups (Keller et al. 2007a). Investigation of the *Ahr* locus, which codes for the receptor through which TCDD acts, did demonstrate an influence on how TCDD affects molar shape (Keller et al. 2007b). The authors were able to identify the amount and timing of TCDD exposure that produced shape alterations in LM1 and LM2 on the basis of the effects of TCDD dosage on different inbred strains of mice with TCDD-sensitive *Ahr* alleles (Keller et al. 2008).

7.5.2 Prediction of tooth shape variation based on developmental models

The patterning cascade model of cusp development, where the position, size, and shape of the earliest-forming cusps affect variation in later-forming cusps (Jernvall 2000; Polly 1998; Salazar-Ciudad and Jernvall 2002), was tested by Skinner and Gunz (2010) in their study of accessory cusps in chimpanzee lower molars. The authors collected three-dimensional landmarks and semi-landmarks from micro-CT models of the EDJ surface to identify correlations between molar crown shape and the presence of a sixth, accessory cusp (C6). Their results indicate that C6 frequency is higher in larger molars and variation is correlated with the location and size of later-forming cusps; the results support their hypothesis that C6 formation would increase with tooth bud size and the accompanying decrease in inhibiting gene products in the bud. Skinner and Gunz (2010) propose that extra cusps beyond C6 represent the same iterative developmental process that produced primary cusps and caution against treating such cusps as traits independent of overall tooth size or adjacent cusp morphology in cladistics.

7.5.3 Developmental constraint

Polly used two Paleogene lineages of viverrid carnivorans (1998) and five modern shrew populations (2005) to explore patterns of dental phenotypic correlation and developmental constraint. Using landmark data from carnivoran LM1s, the author found variability in cusp position significantly correlated with timing of cusp initiation, as well as the amount of intercusp growth and evolutionary change (Polly 1998). The loose local developmental constraint on molar shape suggested by these findings (Polly 1998) was also supported by computer modeling of phenotypic covariance due to developmental interactions in the LM1 of the common shrew (Polly 2005). Polly (2005) concluded that because only a small proportion of the covariance could be explained by development, it is likely that more proximate factors play a larger role in the evolution of molar shape variance.

Renaud et al. (2006) explored internal developmental constraint on molar shape by relating phenotypic covariance and the direction of morphological evolution in fossil rodents, as described by Fourier analysis. They identified an evolutionary "line of least resistance" corresponding to the direction of greatest intraspecific variation and contrasted two lineages: *Apodemus*, which epitomizes this trajectory over the last ten million years, and *Stephanomys*, a pronounced departure from the "line of least resistance" attributable to a

powerful environmental degradation. Functional constraints were considered along with development in a subsequent study of covariation in the molar row of *Mus* and *Apodemus* (Renaud et al. 2009). Strong covariation between adjacent teeth within the molar row was attributed to developmental processes, while strong covariation between occluding molars was explained by functional constraints. It is important to note that the two rodents exhibited a conserved pattern of covariation, despite having diverged more than ten million years ago (Renaud et al. 2009).

Constraint on development (and ultimately tooth morphology) due to the physical space available in the jaw was addressed by Boughner and Dean (2004). The staggered order of molar crown mineralization in the baboon was contrasted with overlap in the cusp mineralization process in chimpanzees, and three-dimensional landmark data from mandibles and molar crypts, crowns, and roots were used to explore the relationship between molar development and jaw space. Contrary to the authors' expectations, trajectories of molar row shape change were indistinguishable across the baboon and two species of chimpanzee; little correlation was seen between relative size of the mandible and the spacing and pattern of development of the molars.

7.5.4 Modularity

Insights to development can also be gained through an examination of covariation between traits and their underlying shared genetic effects. Integrated units identified in this manner are referred to as developmental modules and are characterized by their independence from other modules (Klingenberg 2008). Modularity has been explored in detail using GM in the primate cranium (e.g., Bastir and Rosas 2005; Goswami and Polly 2010) and has recently been addressed in the dentition by several GM studies in mice and voles (discussed later).

Workman and colleagues (2002) collected landmarks from the right and left mandibular molar rows of genotyped inbred mouse strains to identify QTLs associated with tooth row size and shape. They found more QTLs for molar shape than molar centroid size; however, the effects of these QTLs were spread across all three molars, suggesting no individual molar represents a genetically distinct developmental unit. The authors also noted that the QTLs for molar shape were many of the same QTLs identified for mandible shape and cranial dimensions in earlier studies. Leamy and colleagues (2005) explored the genetic basis for FA in the mandibular molar row in the same inbred mice. Their QTL study revealed only two loci affecting shape FA but many combinations of locus pairs exhibiting epistasis for size and shape FA.

Dental modularity and integration between teeth have also been studied by Laffont and colleagues (2009), who collected landmarks from outlines of the three lower molars in the vole species *Microtus arvalis*. The authors assessed covariation in shape between molars and performed a PLS analysis to test the two hypotheses that each molar constitutes a semi-independent module or that the three molars are a single integrated block. Although it was recognized that the molars collectively constitute an integrated unit at the scale of the mandible, three individualized molar modules were identified. Interestingly, covariation was higher between LM1 and LM2 than between either LM1 and LM3 or LM2 and LM3, supporting some developmental independence of the latter molar.

7.6 Case study: GM analysis of hierarchical dental development in *Colobus guereza*

The results of Laffont et al. (2009) bring to light an important methodological consideration for studies of the developmental basis of dental variation, particularly modularity, in primates. In the case of the voles, or any rodents in the superimposition studies reviewed previously, selection and placement of landmarks on the dentition are fairly straightforward given that only two tooth types are present in the jaw, and these types are physically separated by a sizable diastema. In other words, options for landmark configurations include those on a single tooth (i.e., single molar) or on all teeth of a certain type (i.e., molar row), but not landmarks on the entire tooth row because of spatial interruption by the diastema.

We use an example from our own studies of the dentition of Old World monkeys to show that primates can be a useful model for exploring modularity, and consequently, development of the mammalian dentition. The full heterodont dentition of primates not only is a more primitive mammalian configuration compared to that of mice, but presents a greater number of landmark configuration options: with the presence of additional tooth types in the canine and premolar teeth, and without a large diastema, shape can be studied at many hierarchical levels in the primate tooth row. In addition to individual teeth and tooth types, it is possible to examine landmark configurations encompassing any adjacent teeth, including the entire tooth row or the anterior and postcanine dentitions.

The choice of landmark configuration implemented should be tailored to the hypothesis being tested, and it should not be assumed that variation captured in a superimposition at one hierarchical level of the dentition would be the same at a different level. GPA depicts landmark configuration variation

as a composite of the coordinated movements of each landmark, following the resistant-fit least squares function described earlier (Gower 1975; Rohlf and Slice 1990; Siegel and Benson 1982; Sneath 1967); thus, the introduction of new landmarks on additional teeth or a decrease in landmarks as teeth are removed from a configuration will have an effect on the observed shape change at each remaining landmark. To illustrate this effect, we present the superimposition of occlusal landmarks from multiple hierarchical levels of the maxillary dentition of the eastern black and white colobus monkey, *Colobus guereza*. This study serves as a caution to tailor configurations to hypotheses; however, it also provides an example of the utility of GM for testing hypotheses of variation and modularity, based on the multiple different shape analyses afforded by the one-time collection of a large set of landmarks.

7.6.1 Materials and methods

Landmarks were collected from 75 crania curated at the American Museum of Natural History (New York), Cleveland Museum of Natural History (Ohio), and National Museum of Natural History (Smithsonian Institution). We restricted study to adult monkeys with fully erupted third molars to control for ontogenetic variation. Our sample contained 43 males and 32 females.

Specimens were photographed using a Nikon D80 camera with a Nikkor AF-S 105 mm micro lens such that each specimen was oriented with the postcanine occlusal surface in the focal plane. Two-dimensional landmark data were collected from the photographs with the digitizing program tpsDig 2.10 (Rohlf 2006). A total of 93 landmarks were collected, representing overall dental arch shape, but also including shape information for groups of teeth within the row as well as individual teeth. Landmarks are illustrated in Figure 7.2. After bilateral landmarks (all except midline incisor) were reflected across the midline and averaged using program BigFix6 (Sheets 2001a), the total number of landmarks for analyses was 47.

We implemented GPA of the landmark configurations in the program CoordGen6 (Sheets 2001b), followed by principal components analysis (PCA) using PCAGen6 (Sheets 2001c). The PC axes correspond to eigenvectors of the variance-covariance matrix for the shape data, and eigenvalues are proportional to the variance explained by the PCs (Zeldtich et al. 2004). GPA and PCA were carried out at three hierarchical levels: (1) entire tooth row, including 47 landmarks on the incisors, canine, premolars, and molars; (2) postcanine dentition, including 39 landmarks on the premolars and molars; and (3) molar row, including 31 landmarks on the three molars.

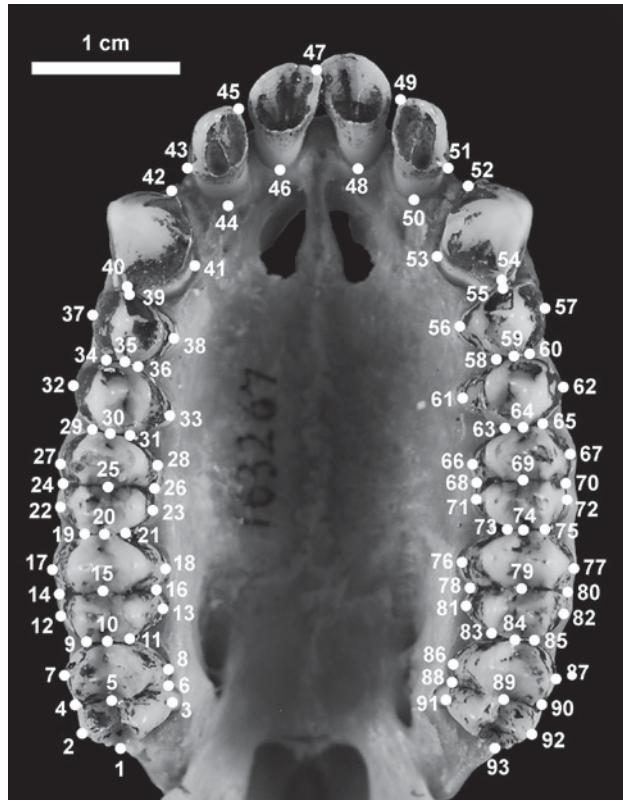

Figure 7.2. Photograph of *Colobus guereza* maxillary dentition illustrating the 93 landmarks collected in the study.

7.6.2 PCA results at three hierarchical levels

The percentage of the total shape variation explained by PC1 is greatest in the analysis at the level of the whole row (36.1 percent), followed by the postcanine level (22.8 percent) and smallest at the molar row level (18.2 percent). In addition, deformation in shape associated with PC1 differs across shared teeth in all three levels. Figure 7.3 illustrates these differences between premolars and molars at the tooth row and postcanine levels and between molars at all levels. In the whole row configuration, the greatest dimension of variation involves a mesiodistal contraction of the entire postcanine dentition, relative to translation and rotation of the anterior dentition. Note that the magnitude of vectors on the incisors and canine are some of the largest in the entire configuration, suggesting that variation in these teeth may be driving the PC1 trend.

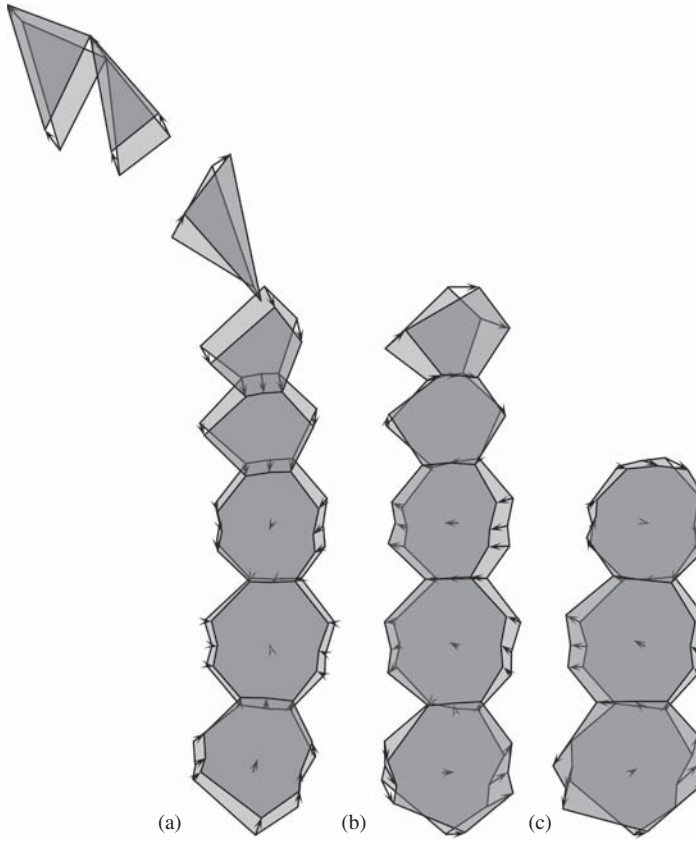

Figure 7.3. Deformations representing the first principal component of shape variation in the maxillary dentition of *Colobus guereza* at the levels of the whole tooth row (a), the postcanine teeth (b), and the molar row (c). Shape change is represented by vectors on landmarks, indicating the deformation from the mean shape (light gray tooth polygons) in one direction along the first principal component axis (dark gray tooth polygons).

Using the coordinated movement of teeth within PC1 as a means of identifying possible modular units, the postcanine dentition, which expands or contracts as a single unit relative to shape changes in the anterior dentition, stands out as a strong candidate. We then analyzed this restricted set of landmarks representing only the postcanine teeth. PC1s for the postcanine (Figure 7.3b) and molar row configurations (Figure 7.3c) present different patterns of shape variation. At the postcanine level, premolars are shifted buccally together, while the first and second molars translate lingually and the third molar rotates distally and buccally. At the level of the molar row, each molar is characterized by a different

pattern of landmark displacement. In summary, the postcanine module identified at the tooth row level is broken down into a premolar module and a separate module composed of the first two molars, with the third molar appearing independent. At the level of the molar row, the coordination between the first two molars is not observed, suggesting independence between each individual tooth.

The shape deformations represented by PC2 demonstrate similar relationships (Figure 7.4). In the whole tooth row configuration, PC2 (14.7 percent of variation explained) represents variation in the mesiodistal position of incisors and the buccolingual position of premolars, all relative to the canine, accompanied by buccal translation of the premolars and first molar and lingual translation of the third molar. In other words, the greatest dimension of variation within the tooth row includes a clockwise rotation of the entire postcanine dentition, relative to an increase in canine width and a mesial translation of the incisors. Note again that the magnitudes of vectors on the incisors are some of the largest in the entire configuration and hence may be driving the PC2 trend as well.

A postcanine module is also suggested by PC2 at the tooth row level, but, as seen for PC1, the integrated movement of teeth at lower hierarchical levels suggests smaller modules within the tooth row as well. At the level of the postcanine dentition, PC2 (10.9 percent explained) depicts extreme mesial compression of the first premolar and buccal translation of the second premolar, in contrast to the coordinated mesiodistal expansion of the molar row as a single unit (Figure 7.4b). PC2 at the molar row level (13.8 percent explained) presents a different aspect of variation, in which molars vary together in buccolingual width (Figure 7.4c).

7.6.3 Modularity in the maxillary dentition of an Old World monkey

On the basis of the coordinated movement of teeth within deformations corresponding to the first and second PCs of shape variation from our GM analysis, we identified several levels of phenotypic modularity. Analysis of landmarks across the entire tooth row consistently demonstrated a dissociation between movement of the anterior and postcanine dentitions, suggesting that each corresponds to a separate module. This phenotypic module corresponds to expectations from the Homeobox Code Hypothesis (Sharpe 1995; Thomas and Sharpe 1998), combined premolar/molar odontogenic field specification in development (Järvinen et al. 2009; Yamanaka et al. 2007; Yamanaka and Uemura 2010), and evidence from quantitative genetic analyses of mice and baboons (Hlusko et al. 2011).

Similarly, when only landmarks on the postcanine teeth were analyzed, the coordinated movement of the premolars could be distinguished from shape

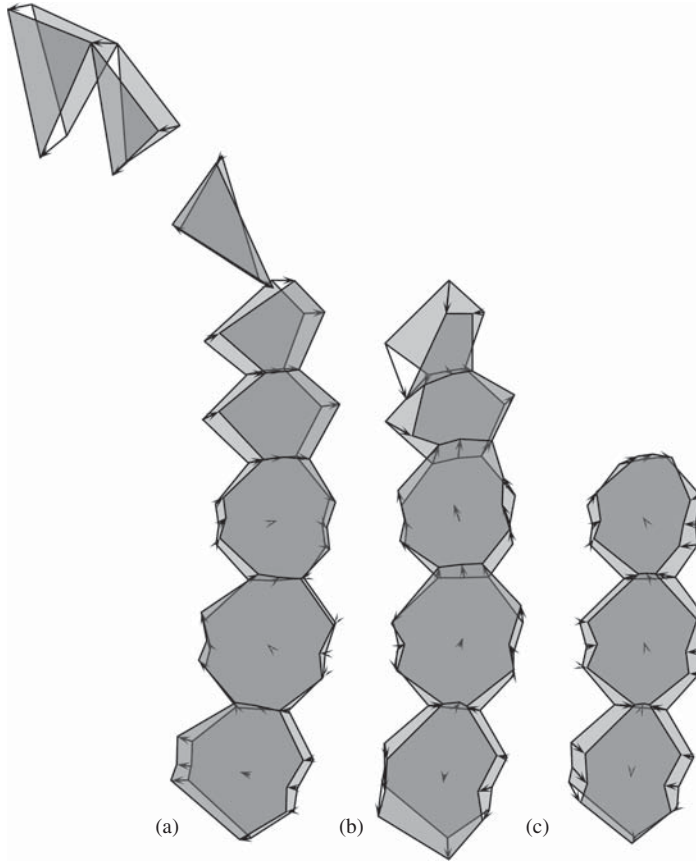

Figure 7.4. Deformations representing the second principal component of shape variation in the maxillary dentition of *Colobus guereza* at the levels of the whole tooth row (a), the postcanine teeth (b), and the molar row (c). Shape change is represented by vectors on landmarks, indicating the deformation from the mean shape (light gray tooth polygons) in one direction along the second principal component axis (dark gray tooth polygons).

change in the molars, indicating that within the postcanine module there exists some independence between tooth types. This also follows evidence from quantitative genetic analyses of baboons (Hlusko et al. 2011; Hlusko and Mahaney 2009) and suggests that some genetic distinction between premolars and molars may characterize all Old World monkeys.

Integration within the molar row is more complicated: at the levels of the postcanine dentition and molar row, independence between molars, particularly in the case of the third molar, was observed in the first PCs, while in the

second PCs, which account for a smaller portion of the total shape variation, molars change shape in a coordinated fashion, reinforcing the idea of a single molar row module. Quantitative genetic analyses of variation in baboon molar cusp orientation suggest that there may be modules within and across the molar row (Hlusko et al. 2004). Combining this quantitative genetics work with what is coming out of mouse developmental genetics, and the possibilities inherent in the significant amount of primate skeletal material around the world, many interesting research directions are ripe for exploration.

7.7 Conclusions

One of the essential questions in the study of skeletal morphology concerns the definition of "phenotype," not in the classic sense of the relationship between genes and environment, but in terms of how one should define a phenotype at the anatomical level to address a research question most accurately (e.g., Hlusko 2004; Houle 2001; Wagner and Laubichler 2001). "The phenotype" is often a proxy for understanding how genes, environment, and evolution interacted and is therefore a fluid concept that depends on the research question. For example, a question about function may necessitate a view of the hominid pelvis and hip joint as one interrelated unit (e.g., Lovejoy et al. 1999), whereas a question about how selection or drift resulted in loss of the third molar in marmosets and tamarins requires an investigation of either the mechanisms that pattern variation within the molar series specifically or the length of the dental lamina at the level of the tooth row. Which is the more representative phenotype?

GM is a powerful tool in that it enables the phenotype to be defined variably, and experimentally. As such, definition of "the phenotype" can be explored at multiple levels and for multiple research aims. Primates offer a particularly useful taxonomic group within mammals for this type of research given their geographic breadth and diversity, and the fortuitous assemblage of specimens in museum collections. Add in the depth of our understanding about developmental genetics of mammalian teeth, and GM analyses of primate dental variation will be a fruitful tool in evolutionary biology for many years to come.

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8 *Evolution of hominin postcanine macromorphology: a comparative meta-analysis*

KES SCHROER AND BERNARD WOOD

8.1 Introduction

Researchers of human evolution have devoted considerable effort to documenting the macroscopic morphology of the postcanine dentition of taxa within the human clade. Postcanine macroscopic morphology has been used to assign individual fossils to taxa, reconstruct the possible diets of fossil hominins, develop hypotheses about evolutionary trends within the human clade, and help reconstruct hominin phylogeny. Some of these studies have drawn on comparative data to help polarize the character states of postcanine dental traits, but most have made a priori assumptions about the morphocline of postcanine macromorphology. Such studies have been based on the expression of these characters in either a taxon researchers have assumed is the stem hominin or a taxon that is assumed to be more primitive than the taxon, or taxa, under consideration.

In this review, we use the concept of the ancestral morphotype to generate a number of hypotheses, the central one being a hypothesis about the macromorphology of the postcanine dentition of the most recent common ancestor of modern humans and chimpanzees/bonobos. We inform that hypothesis by considering the postcanine tooth macromorphology of extant and fossil members of the African ape clade, including members of the human lineage. We then compare our hypothesis about the ancestral morphotype with the morphology seen in several fossil taxa that have been proposed as either the common ancestor of all hominins or the earliest member of the hominin clade.

If the morphologies of extant sister taxa have diverged substantially from their most recent common ancestor, it can be challenging to retrodict the ancestral morphology from the extant states (Andrews and Harrison 2005). In

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cases where various lines of evidence suggest that two taxa are divergent, then the predicted ancestral morphotype can be an inaccurate approximation of the true ancestral condition (Wood and Harrison 2011). In the case of hominins, the temptation is to assume that the traits that distinguish modern humans from the extant great apes are related to the uniqueness of modern humans. However, the Miocene precursors (N.B.: by precursors we do not mean to imply they are literal ancestors) of the extant great apes and modern humans were anatomically, and presumably behaviorally, quite different from modern great apes (Begun et al. 2012). Many of the traits associated uniquely with modern humans may also be primitive retentions or even morphologies that are homoplasic in a broader context (Diogo and Wood 2011).

Since the extant apes and modern humans represent relict and probably highly specialized terminal members of what was once a diverse radiation of apes (Andrews and Harrison 2005; Suwa et al. 2009; Wood and Harrison 2011), the reconstruction of ancestral morphotypes within the great ape clade has been challenging. However, the alternative to developing and testing hypotheses about ancestral morphotypes is even less appealing, for it is the *ex cathedra* pronouncement that a fossil taxon *is* the stem taxon of a clade (White et al. 2009). We prefer the uncertainties of the former strategy to the obvious pitfalls that are inevitable with the latter one.

If one of the several purported earliest hominin taxa is consistent with predictions about the ancestral morphotype, then all is well and good. But what happens, as was the case with *Ardipithecus*, when the stem hominin taxon contradicts the hypothetical ancestral morphotype? The assumption that *Ardipithecus* is the stem taxon of the human clade necessitates "a spectacular amount of homoplasy" among the extant great apes, especially in aspects of suspensory morphology (Begun 2010). However, if *Ardipithecus* is *not* the stem taxon of the human clade, then it would require parallel evolution between *Ardipithecus* and undoubted hominins. Both scenarios appeal to Occam's razor, but whereas the former appeal is more inclusive and hominoid-centric, the latter appeal is more exclusive and hominin-centric.

Rather than rely upon *post hoc ergo propter hoc* (after, therefore because of) descriptions of the ancestral taxon of the human clade, we have generated a series of a priori evolutionary hypotheses about the primitive and derived traits of the macromorphology of the postcanine dentition based on observations from closely related extant taxa and their fossil relatives. In this chapter, we present predictions about the probable postcanine macromorphology of the most recent common ancestors of modern humans and the African apes, of modern humans and chimpanzees/bonobos, and of the stem hominin. We then assess how well the last prediction is matched by the postcanine macromorphology of proposed fossil hominins.

We use the term "hominin" to refer to modern humans and their close fossil relatives, a custom of many authors (Begun 2007; Richmond 2000; Strait and Grine 2004; Wood 2010). However, we recognize that "hominin" is not an ideal taxonomic term, as it refers to being a member of the Hominini, the tribe that some have argued includes chimpanzees, bonobos, and modern humans (e.g., Andrews and Harrison 2005). The use of a single tribe for both modern humans and chimpanzees/bonobos acknowledges the close molecular and morphological relationship (Chen and Li 2001; Diogo and Wood 2011; Ebersberger et al. 2002; Pilbeam 2002) to the exclusion of their nearest shared relative, gorillas (but see Scally et al. 2012, for evidence of a minority of genes shared between modern humans and gorillas). In this schema, the human lineage would be a subtribe and the appropriate vernacular for members of the exclusively human lineage would be homininan (from the subtribe Hominina) and the vernacular for members of the chimpanzee/bonobo lineage would be paninan (from the subtribe Panina). But to prevent unnecessary confusion, we follow past practice and refer to modern humans and members of their lineage as hominins and chimpanzees/bonobos and members of their lineage as panins (Figure 8.1). When we refer to the subfamily Homininae (*Homo*, *Pan*, *Gorilla*), we use the vernacular term "hominine"; when we refer to the family Hominidae (Homininae plus their nearest relative, *Pongo*), we use the vernacular term "hominid"; and when we refer to the superfamily Hominoidea (Hominidae plus gibbons and siamangs), we use the vernacular term "hominoid."

The term "most recent common ancestor" (MRCA) refers to a population or representative sample (not a specific individual) of the population that was

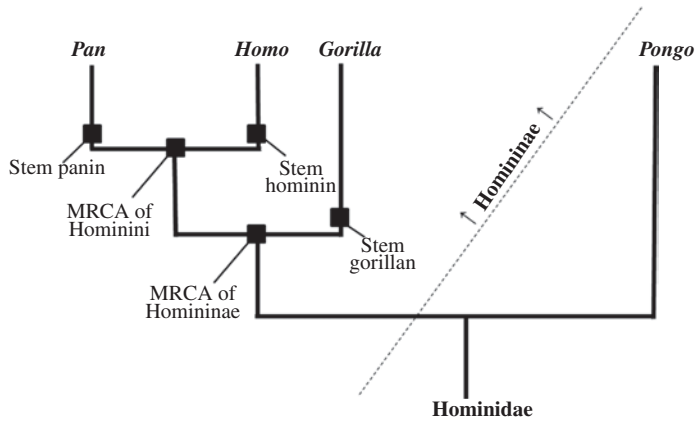

Figure 8.1. Cladogram demonstrating the proposed evolutionary relationship between extant hominines and their closest relative, *Pongo*. Black boxes indicate key fossil relatives such as ancestors and stem taxa in reference to their modern relatives.

ancestral to two lineages before their evolutionary divergence. When discussing the proposed character states of this population, or of any taxonomic group, we use the term "primitive" to mean general (i.e., ancestral or basal) traits that are shared by most or all members of a clade. The term "primitive" does not imply any evaluation of the evolutionary worth of a trait. The subclade that includes the extant taxon is called the "crown group"; the remaining taxa compose the "stem group." All taxa within the stem group are stem taxa, but there has to be an initial taxon within the stem group; we refer to this as the "stem taxon."

Although traits associated with posture, locomotion, dexterity, and cognition are likely to have been at least as, if not more, adaptively significant as postcanine macromorphology, the vagaries of preservation are such that we are less likely to find evidence of them in the fossil record. Postcanine teeth are either the most common or among the most common parts of the body preserved in mammalian fossil assemblages (Grine and Martin 1988). Indeed, some hominin fossil assemblages (e.g., Omo-Shungura) and some hominid taxa (e.g., *Dryopithecus brancoi*) are composed almost exclusively of dental and gnathic remains. In the unlikely event that the fossil evidence of the MRCA of hominins and panins is found, it is likely that the specimen(s) involved will include evidence of postcanine tooth morphology.

8.2 Materials

When considering the polarity of postcanine macroscopic morphology, advances in genetics and evolutionary development remind us that molecularly close relatives have not necessarily undergone the same amount of morphological change since their divergence from a common ancestral population. It may be that a more distant relative might be a better model for the morphology of the common ancestor if it can be demonstrated that less morphological change has accumulated in that relative since its divergence from the most recent common ancestor of the more inclusive taxonomic group (Jenner and Wills 2007). For this reason, we look at postcanine macromorphology of the hominins and panins in a comparative context that includes their closest living relative (gorillas) and several extinct hominine taxa (Table 8.1). We also include *Pongo* as a comparator for all hominines.

8.3 Methods

We restrict our postcanine sample to permanent dentitions. Since pooled sex samples discriminate among extant hominoid species and subspecies in the

Table 8.1. *Extant hominids plus fossil hominines*

Family Hominidae (hominids)
Subfamily Ponginae (pongines)
Genus ***Pongo***
Subfamily Homininae (hominines)
Tribe Gorillini
Genus ***Gorilla***
Tribe Hominini
Genus ***Pan***
Genus *Australopithecus**
Genus *Kenyanthropus**
Genus *Paranthropus**
Genus ***Homo***
Tribe *incertae sedis*
Genus *Chororapithecus*
Genus *Samburupithecus*
Genus *Ardipithecus*†
Genus *Orrorin*†
Genus *Sahelanthropus*†

Notes: Extant hominids are shown in boldface.
* These are almost certainly early hominins.
† These are purported early hominins.

main, we do not address sex differences (Pilbrow 2003). Premolars and molars represent different tooth classes with different developmental origins (Ash and Nelson 2004). Although the macromorphology of premolars and molars likely reflects an integrated adaptation to diet (Lucas 2004), the relative independence of developmental pathways of the two tooth types suggests they should be treated separately for the purposes of this review. Likewise, although upper and lower dentitions must be integrated to produce effective chewing, the two dentitions develop under the control of different molecular pathways; thus, for similar reasons to those given earlier we review the maxillary and mandibular teeth separately (Ferguson et al. 2000). We limit our analysis to the macromorphology of the crown and root; we do not consider any microstructural variables. The variables we consider are nonmetric, or if they are metric, they refer to relative size of the crowns or main cusps (Figure 8.2).

Taxonomic affiliations are more difficult to determine (and phylogenetic relationships are more difficult to reconstruct) for taxa for which there is relatively little morphological evidence and no molecular evidence. For these reasons, we consider fossil-only taxa separately from extant hominines, for which an abundance of both types of evidence is available. Nevertheless, despite the paucity of evidence, fossil-only taxa provide a potentially important additional source of information concerning morphological diversity of hominines, and

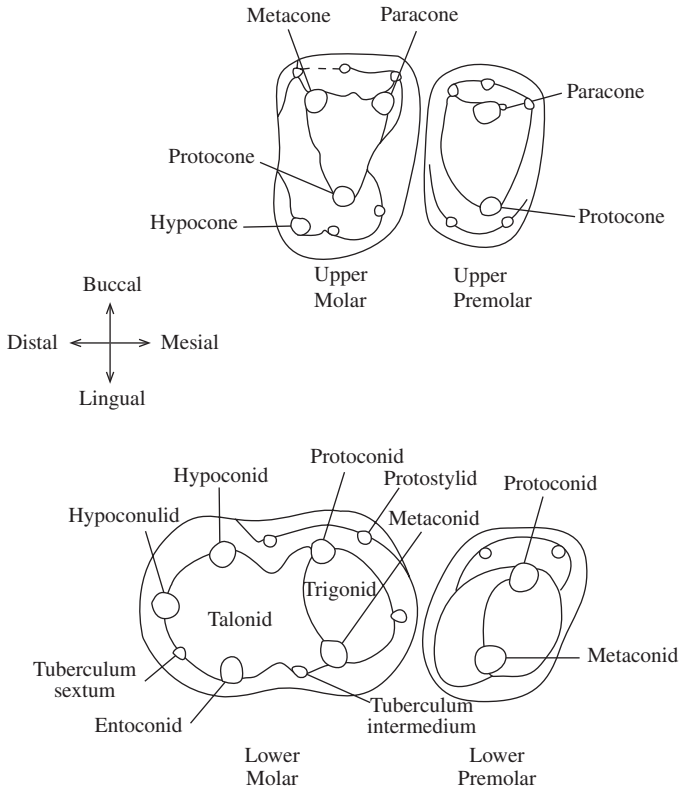

Figure 8.2. Diagram indicating important features of the occlusal surfaces of upper and lower postcanines. Cusps are indicated by large circles. Outlines after Swindler (1978).

help provide some chronological control for the emergence of derived traits in extant hominine taxa.

We use the comparative method to develop hypotheses about primitive and derived states of nonmetric traits in the MRCA of all hominines, in the MRCA of hominins and panins, and in the stem taxon of extant hominines. We then review postcanine macromorphology of purported hominins in light of these predictions. Although the designations of primitive and derived states inevitably oversimplifies the complex interactions involved in development, selection, and adaptation, they allow researchers to generate testable hypotheses of hominin phylogeny (Begun 2007). In particular, they allow us to make predictions about the presence of homoplasy, that is, the presence of similar morphologies in closely related taxa that are not seen in their most recent common ancestor (McHenry 1996). Ancestral morphotypes informed by our extant and

fossil comparisons should reflect primitively shared traits of all descendant lineages of that population (Wood and Harrison 2011).

8.4 Results and discussion

The results of our comparative meta-analysis of postcanine macromorphology of extant and fossil taxa are summarized in Tables 8.2 through 8.6 (these data are from citations later and Berger 2010; Beynon and Wood 1986; Kinzey 1984; Pilbrow 2003; Scott and Turner 2000; Swindler 2002; Uchida 1993; Ungar 2010; Wood and Abbott 1983; Wood et al. 1988).

8.4.1 Postcanine macromorphology of the MRCA of hominines: predictions based on extant taxa

Like that of all Old World anthropoid primates, the hominine postcanine dentition has two premolars and three molars in each quadrant. Crowns of hominine postcanine teeth are generally elongated. Lingual cingula development is variable within this clade, but buccal cingula are rare or absent in most taxa.

Molars of hominines are distinct from those in other primates because of the rounded form of the crown profile (i.e., bunodont), and upper and lower M1s and M2s are relatively similar in size. Upper molars are typically four-cusped with a prominent paracone, a large protocone, and sometimes a large metacone; the main cusps are separated by a distolingual groove, and there is a well-defined diagonal crest (i.e., crista obliqua). The pattern of fissures between the main cusps of lower molars is typically described as Y-5. Lower molars typically have a large talonid behind a crest, the protocristid, which connects the protoconid and metaconid. In the lower molars of most individuals, the metaconid of the LM1 is opposite, or distal to, the protoconid. A postprotocristid connecting the entoconid and hypoconid forms the boundary of a post-talonid basin. Two extra cusps may develop in lower molars: a C6 (i.e., entoconulid or tuberculum sextum) and/or a C7 (metaconulid or tuberculum intermedium); their rates of occurrence differ among hominine taxa. Maxillary molars of hominines generally have three roots and the lower molars two roots.

Hominine upper premolars are oval and bicuspid with a well-developed protocone on the UP2. Paracones of both upper premolars are larger than the protocones. Transverse crests connecting the two cusps separate the occlusal surface into three regions, or foveae. The LP1 is sectorial in all extant hominine taxa other than modern humans, and the metaconid may equal, or exceed, the size of the protoconid. As in most Old World primates, the hominine LP1 sharpens

Table 8.2. *General characteristics of postcanine macromorphology in extant and fossil hominines and Pongo*

	Pongo extant	*Gorilla* extant	*Pan* extant	*Homo* extant	*Paranthropus* 2.7–1.2 mya	*Australopithecus* 4.2–1.95 mya	*Kenyanthropus* 3.5 mya	*Ardipithecus* 5.6–4.4 mya	*Orrorin* 6.2–5.8 mya	*Sahelanthropus* 7 mya	*Samburupithecus* 9.6 mya	*Chororapithecus* 10.5–10 mya
Relative crown size	Large	Large	Intermediate	Small	Very large	Large, but small in *Au. sediba* and very large in *Au. garhi*	Small UM1 and UM2	P2-M1 are intermediate, M2-M3 are large	Small	Intermediate	Large	–
Crown relief	Low	High	Low	Low	Low	Low, but intermediate in *Au. africanus*	Low	Low	Low	Low	Intermediate	Intermediate
Enamel crenulations	Pronounced	Slight	Slight	Absent?	Absent?	Slight?	Slight	Slight?	Slight	Slight	–	–
Peripherally located cusps	No	No	Yes	No	No	No	No	No	No	No	No	Yes
Expansion of mesial fovea	None	None	Broad	None	None	None	None	Intermediate	None	None	Intermediate	Intermediate
Basal crown flare	No	No	No?	Yes	Yes	Yes	Yes?	Yes	–	Yes?	–	–
Molar crown size order (most common pattern)	M1<M2>M3	M1<M2>M3	M1<M2>M3 and M1>M2>M3; M3s often reduced	M1>M2>M3, but M1<M2>M3 in early *Homo*; M3s often reduced	M1<M2<M3	M1<M2<M3	–	M1<M2>M3	–	M1<M2>M3	–	–
Enamel thickness	Thick	Very thin	Thin	Very thick	Very thick	Thick	Thick	Intermediate	Thick	Intermediate	Thick	Thick

Table 8.3. *Characteristics of upper molar macromorphology in extant and fossil hominines and Pongo*

	Pongo extant	*Gorilla* extant	*Pan* extant	*Homo* extant	*Paranthropus* 2.7–1.2 mya	*Australopithecus* 4.2–1.95 mya	*Kenyanthropus* 3.5 mya	*Ardipithecus* 5.6–4.4 mya	*Orrorin* 6.2–5.8 mya	*Sahelanthropus* 7 mya	*Samburupithecus* 9.6 mya	*Chororapithecus* 10.5–10 mya
Broad crowns?	In mesial aspect only	Yes	No	No	Yes, very broad	Yes	–	No	–	–	–	–
Relative size of the hypocone	Large	Very large	Small	Small	Large	Small	–	–	–	–	–	–
Anterior fovea	Yes	Yes	Yes	No	Yes	Yes		Yes	–	–	–	–
Distolingual groove	Pronounced	Pronounced	Weak	Absent	–	Weak		Weak	–	–	–	–
Buccal cingula	Rare	Rare	Sometimes present in *P. troglodytes*	Uncommon in modern humans	Weak	Intermediately expressed	–	–	–	–	–	Weak
Lingual cingula	Common	Common	Common	Uncommon	Weak	Intermediately expressed		–	Absent	–	Yes, intermediate in size	Weak
Other accessory structures	Protoconules and metaconules sometimes present	Protoconules and metaconules sometimes present	Distoconule sometimes present in *P. troglodytes*	None	Distal cuspule common	–	–	–	–	–	–	–
M3 shape	Trapezoidal	Square	Square	Square	Square	Square	–	Rectangular	Triangular	–	–	–
M3 distal taper	No?	No?	No?	Yes	Yes	Yes	–	No	–	–	–	–
Distal fovea on distobuccal corner of M3	Yes	Yes	No	No	–	No	–	No	Yes	–	–	–
Molar root number	3	3	3 (sometimes 2, especially in M3)	3 (often fused or partially fused)	3	3	–	3	–	–	–	–

Table 8.4. *Characteristics of lower molar macromorphology in extant and fossil hominines and Pongo*

	Pongo extant	*Gorilla* extant	*Pan* extant	*Homo* extant	*Paranthropus* 2.7–1.2 mya	*Australopithecus* 4.2–1.95 mya	*Kenyanthropus* 3.5 mya	*Ardipithecus* 5.6–4.4 mya	*Orrorin* 6.2–5.8 mya	*Sahelanthropus* 7 mya	*Samburupithecus* 9.6 mya	*Chororapithecus* 10.5–10 mya
M1: position of metaconid	Level with or distal to protoconid	Distal to protoconid	Level with or distal to protoconid	Level with protoconid	Level with protoconid	Level with protoconid (except *Au. sediba*)	–	Level with protoconid	–	–	–	Equal to protoconid
M1 and M2: Crown shape	Elongated	Elongated	Elongated	Broad	Broad	Broad	–	Broad	–	–	–	Elongated
Relative contribution of the talonid	Intermediate	Large	Small	Small	Very large	Small	–	Small	–	–	–	–
Separation between metaconid and entoconid	Shallow	Deep	Deep	Very shallow	Shallow	Shallow	–	–	–	–	–	–
M3: distal taper	Yes	Yes	No	No	No	Intermediate	–	No	–	No	–	Yes
Expression of posterior fovea	Yes	Yes	Yes	No	Yes	Yes	–	– –	–	–	–	–
Buccal cingulids	Common	Common	Common	Uncommon	–	–	–	–	–	–	–	Weakly expressed
Lingual cingulids	Rare	Rare	Rare	Rare	–	–	–	–	–	None	–	Weakly expressed
Protostylid	Weak	Weak	Weak	Common	Common in *P. robustus*	Common in *Au. africanus*	Well-developed	–	–	–	–	–
Extra cusps	C6 or C7 sometimes present	C6 or C7 common	C6 sometimes present in *P. troglodyte*	C6 sometimes present on M2	C6 common; C7 sometimes present, often in conjunction with C6	C6 sometimes present on M2; C7 common	–	–	–	–	–	–
Root number	2	2	2	2	2	2	–	–	–	2	–	–

Table 8.5. *Characteristics of upper premolar macromorphology in extant and fossil hominines and Pongo*

	Pongo extant	*Gorilla* extant	*Pan* extant	*Homo* extant	*Paranthropus* 2.7–1.2 mya	*Australopithecus* 4.2–1.95 mya	*Kenyanthropus* 3.5 mya	*Ardipithecus* 5.6–4.4 mya	*Orrorin* 6.2–5.8 mya	*Sahelanthropus* 7 mya	*Samburupithecus* 9.6 mya	*Chororapithecus* 10.5–10 mya
P1: symmetry	Low	Low	Low	High	High	High, but low in *Au. garhi*	–	Low	–	–	–	–
P1: size of paracone	Tall, but may be equal to protocone	Tall and elongate	Tall and elongate	Equal to protocone	Equal to protocone	Intermediate	–	Intermediate	–	–	–	–
P1: mesiobuccal line extension	Yes	Yes	Yes	Rare	Absent	Common in *Au. afarensis*, absent *in Au. garhi*	–	–	–	–	–	–
P1: mesial triangular portion	Yes	Yes	Yes	No	No	–	–	Yes	–	–	–	–
P2: shape	Oval	Oval	Oval	Trapezoidal	Oval	Oval	–	Rectangular	–	–	–	–
P2: relative contribution of the talonid	Small	Large	Small	Small in late *Homo*; intermediate in early *Homo*	Very large	Minor in most taxa, large in *Au. garhi* and *Au. africanus*	–	–	–	–	–	–
Buccal grooves	No	Yes	No	Weak, except for *H. rudolfensis*	Weak, but pronounced in *P. robustus*	Pronounced	–	–	–	–	–	–
Buccal cingula	Rare	Rare	Absent	Weak	–	–	–	–	–	–	–	–
Lingula cingula	Absent	Common	Rare	Weak	–	–	–	–	–	–	–	–
Accessory cusps	Hypocone and metacone common on P2	Small hypocone sometimes present on P2	Rare	Rare	Buccal cuspule present	–	–	–	–	–	–	–
P1: root number	3 (sometimes 2)	3	3 (sometimes 2)	1 (sometimes 2 or 3)	3 (sometimes 2)	2 (sometimes 3)	3	–	–	2	3	–
P2: root number	3 (sometimes 2)	3	2 (sometimes 3)	1	3 (sometimes 2)	2 (sometimes 3)	3	–	–	2	3	–

Table 8.6. *Characteristics of lower premolar macromorphology in extant and fossil hominines and Pongo*

	Pongo extant	*Gorilla* extant	*Pan* extant	*Homo* extant	*Paranthropus* 2.7–1.2 mya	*Australopithecus* 4.2–1.95 mya	*Kenyanthropus* 3.5 mya	*Ardipithecus* 5.6–4.4 mya	*Orrorin* 6.2–5.8 mya	*Sahelanthropus* 7 mya	*Samburupithecus* 9.6 mya	*Chororapithecus* 10.5–10 mya
P1: symmetry	Low	Low	Low	High	High	Intermediate	–	Intermediate	–	–	–	–
P1: relative size of protoconid	Large	Large	Intermediate	Small	Small	Intermediate	–	Large	–	–	–	–
P1: buccal slope	Steep	Steep	Steep	Rounded	Rounded	Intermediate	–	Steep	–	–	–	–
P1: mesiobuccal projection of crown base	Strong	Strong	Strong	Weak	Weak	Weak	–	Intermediate	–	Strong	–	–
P1: honing facet	Yes	Yes	Yes	No	No	No	–	Yes in *Ar. kadabba*	–	–	–	–
P1: termination of mesial protoconid crest	Less occlusal	Less occlusal	Less occlusal	More occlusal	More occlusal	More occlusal	–	More occlusal	–	–	–	–
P1: mesial marginal ridge	Intermediate	High	Intermediate	Low	High	Low	–	Low	–	–	–	–
P1: relative position of the metaconid	Distal to protoconid	Distal to protoconid	Distal to protoconid	Mesial to protoconid	Mesial to protoconid	Equal to protoconid	–	Equal to protoconid	–	–	–	–
P2: relative contribution of the talonid	Intermediate	Large	Small	Small	Very large	Intermediate	May be large	Large in *Ar. kadabba*	–	Large	–	–
P2: buccal slope	Vertical	Vertical	Intermediate	Rounded		Rounded	–	Intermediate	–	–	–	–

(*continued*)

Table 8.6. (*cont.*)

	Pongo extant	*Gorilla* extant	*Pan* extant	*Homo* extant	*Paranthropus* 2.7–1.2 mya	*Australopithecus* 4.2–1.95 mya	*Kenyanthropus* 3.5 mya	*Ardipithecus* 5.6–4.4 mya	*Orrorin* 6.2–5.8 mya	*Sahelanthropus* 7 mya	*Samburupithecus* 9.6 mya	*Chororapithecus* 10.5–10 mya
P2: crown shape	Elongate	Elongate	Oval	Oval, narrowed	Molariform, narrowed in *P. boisei*	Oval, narrowed	–	Oval	Elongate	–	–	–
Transverse crests	Weak	Weak	Weak	Strong	Weak	Strong	–	Strong	–	–	–	–
Buccal grooves	No	No	No	Yes	Yes	Yes	–	No	–	Yes	–	–
Extra cusps	Hypoconid and entoconid may be present on P2	Hypoconid may be present on P2	Rare	Distolingual cusp may be present on P2	P1 may have additional cusp(s), P2 always has a distolingual cusp and often has a further additional cusp	Distolingual cusp may be present on P2	–	–	–	–	–	–
P1: root number	2 (sometimes 1)	2	2 (sometimes 1)	1	2 (sometimes Tomes' root)	1 (sometimes Tomes' root)	–	2	–	2 (sometimes with 3rd root fused)	–	–
P2: root number	2	2	2	1 (sometimes 2) in late *Homo*; 2 in early *Homo*	2 (often 3)	3 or 2	–	2–3?	–	2 (sometimes with 3rd root fused)	–	–

(or hones) the upper canine as the mouth is opened and closed. Although they possess this honing complex, hominines trend toward decreased expression of this trait, and the upper and lower P1s and P2s tend to be more similar in shape. The LP2 is biscuspid, with a large protoconid and metaconid. A protocristid between these cusps on the LP2 marks the division of the occlusal surface into the trigonid mesially and the talonid distally. Premolar roots are variable in number and form, but most upper premolars have three and most lower premolars have two in number.

This description of hominine postcanine macromorphology provides a baseline definition for the postcanine dentition of the MRCA of hominines but does not provide a diagnosis of the MRCA. Primitive traits of the postcanine macromorphology of the MRCA of the hominines are not notably different from primitive traits for hominid postcanines. On the basis of comparison to extant taxa, it would be difficult to sort the MRCA of the hominines from a fossil hominid. Inclusion of derived traits in the postcanine macromorphology of hominines would aid in differentiating the MRCA of hominines from that of fossil hominids; however, each of the three extant hominine genera is independently derived in its postcanine macromorphology and therefore does not provide a comprehensive picture of the suite of postcanine traits shared by all hominines (see the section on stem taxa). Probable hominine taxa are known from the fossil record, however, and they have the potential to provide information about the likely traits of the MRCA of hominines.

8.4.2 Postcanine macromorphology of the MRCA of hominines: predictions based on fossil taxa

One candidate for an early hominine is *Chororapithecus abyssinicus*, a taxon known from isolated fossil teeth found in Ethiopia dated to 10.5–10 Ma (million years ago). Although its discoverers argue that the possible slicing crest on one molar suggests *Chororapithecus* is a close relative of gorillas (Suwa et al. 2007), its teeth are generally different in their gross morphology and functional anatomy (Begun 2010). *Chororapithecus* has lower relief than do modern gorillas; it also shares some traits with hominins and panins, including somewhat peripherally located cusps surrounding the consequentially expanded occlusal basins, thick enamel, and weakly expressed cingula (Suwa et al. 2007). These traits suggest *Chororapithecus* is more likely an early hominine than a member of the gorilla clade.

A second possible early hominine is *Samburupithecus kiptalami*, a taxon known from localities that sample apparently woody habitats in East Africa dated to 9.6 Ma (Ward and Duren 2002). The postcanine teeth feature pronounced

lingual cingula as in gorillas; crown relief is intermediate (i.e., between that of early hominins and gorillas), and the mesial foveae less broad than in chimpanzees but wider than in humans and gorillas (Ishida and Pickford 1997). Molars increase in size mesially to distally in the way they do in *Australopithecus* and *Paranthropus*.

Some isolated fossil teeth found in East Africa also have affinities to the hominines, but they have not yet been referred to any fossil or extant species. The Kapsomin ape teeth include BAR 1757'02, a 5.9 Ma upper molar that is relatively large and within the range of *Australopithecus*. Its thin enamel, higher cusp relief, unflared buccal surface, and small crenulations suggest a linkage to the gorilla clade (Pickford and Senut 2005). The Kapsomin molar provides evidence that a hominine was living at the same time and place as *Orrorin*, a possible hominin we discuss later.

Chimpanzee-like teeth from the Ngorora Formation of Kenya date to ca. 12.5 Ma. The Ngorora lower molar (BAR 91'99) is similar to that of chimpanzees in its somewhat peripherally located cusps; however, the molar also has a well-defined buccal cingulum and mesial fovea that is narrower than in chimpanzees (Pickford and Senut 2005). It is tempting to suggest that the Ngorora lower molar is from an early form of chimpanzee, but it dates well before what we understand to be the revised timing of the proposed split between human and chimpanzee lineages (Langergraber et al. 2012). If that understanding were to change to an even earlier time, then resemblances to extant chimpanzees may be homologies. The Cheboit lower molar (BAR 2000'03), which dates to 5.9 Ma, is close to the proposed period for the human and chimpanzee split and also has peripherally located cusps. Unlike the Ngorora molar, this cusp form is coupled with a large mesial fovea as is the case in modern chimpanzees. The trapezoidal shape of the Cheboit molar and its reduced hypoconulid also link it with panins and suggest it might be a third molar of an early panin taxon (Pickford and Senut 2005)

Though fossil data are sparse, they provide some insight into the traits shared primitively among all hominines, particularly the peripherally located cusps in *Chororapithecus* and the Ngorora and Cheboit lower molars. These remains suggest that this type of macromorpholgy may not be restricted to extant panins. It is reasonable to deduce that somewhat peripherally-located cusps may be a primitive hominine trait, with a well-pronounced expression emerging in panins soon after the split from an ancestral population shared with hominines. In this scenario, peripherally located cusps would have become more centrally located over time in the human and gorilla lineages.

The presence of intermediate crown relief in most African ape fossils suggests this trait is primitive for the hominine clade, with the human and chimpanzee lineages showing a reduced expression compared to the MRCA of hominines and the gorilla lineage showing an increase in expression. From

a consideration both of extant hominines and of probable fossil hominines, we hypothesize that the postcanine macromorphology of the MRCA features general hominid traits potentially combined with higher crown relief and more peripherally located cusps.

8.4.3 Postcanine macromorphology of the MRCA of hominins and panins: predictions based on extant taxa

Members of the tribe Hominini share a general trend of reduced complexity (e.g., cusp number, root number) of postcanine macromorphology compared to the hominine condition. In modern humans and chimpanzees/bonobos, M3s of the upper and lower dentitions are reduced in size and often lack the most distal cusp; the teeth may also be absent. In the upper molars, hypocones are reduced and distolingual grooves and distal foveae are either absent or weakly expressed. Upper and lower molars nearly always decrease in size distally in modern humans, and this pattern is more frequently found in chimpanzees than any other hominid (Mahler 1980). In the premolars of modern humans and chimpanzees/bonobos, the LP1 is more symmetrical with a more weakly expressed honing complex; in modern humans the honing complex has been lost. Root number in both the upper and lower premolars is often decreased in modern humans and chimpanzees, especially so in modern humans, who often have single-rooted teeth (Abbott 1984; Kupczik 2009). Any fossil hominine with markedly reduced crown complexity in the upper and lower M3, more symmetrical LP1 crowns, and reduced root number is at least a candidate for being the MRCA of hominins and panins, unless there is other evidence to suggest these features are homoplasic.

8.4.4 The postcanine macromorphology of the MRCA of hominins and panins: predictions based on fossil taxa

We are hampered by the lack of early (i.e., pre-2 Mya) fossils attributed to the panin clade, although there is important, but unfortunately meager, recent fossil evidence from 545,000 years ago of chimpanzees living in East Africa (McBrearty and Jablonski 2005). However, evidence of one or more adaptive radiations of hominins is known from fossil sites in East, southern, and Central Africa. Fossils of these localities provide critical insights into the evolution of postcanine macromorphology within the hominin clade. The earliest undisputed hominin, *Australopithecus anamensis*, is known from East Africa and dates to ca. 4.2 Ma (Ward et al. 1999). The genus *Australopithecus* currently includes

five additional species – *Australopithecus afarensis* (also from East Africa and probably a later segment of a chronospecies that includes *Au. anamensis*), *Australopithecus africanus* (a southern African species dating to 2.8–2.5 Ma), *Australopithecus sediba* (a younger, ca. 2 Ma, southern African species and possible regional variant of *Au. africanus*), *Australopithecus bahrelghazali* (known from deposits in Chad ca. 3.6 Ma), and *Australopithecus garhi* (an East African taxon dating to 2.5 Ma). For a variety of reasons, researchers have concluded that the genus *Australopithecus* is almost certainly paraphyletic (Strait and Grine 2004).

The upper molars of *Australopithecus* are broader than in either extant hominins or panins; however, they share with extant hominins and panins to the exclusion of other hominines the tendency to have smaller hypocones, weakly expressed distolingual grooves, and square distal molars with a weakly expressed distal fovea (Wood and Engleman 1988). A C6 may also be present in the LM2s of *Australopithecus*, and C7s and well-developed protostylids are common. Upper and lower molar crowns may have bulging sides; this trait is especially prominent in *Au. anamensis* and is shared with later *Paranthropus*. The postcanines of *Australopithecus* have thicker enamel than do those of gorillas or chimpanzees; this trait is possibly part of an evolutionary trend toward the hyperthick enamel of *Paranthropus* and *Homo*.

Compared with those of hominines, premolars of *Australopithecus* are somewhat buccolingually narrowed, a trait shared with modern humans. Upper premolars of *Australopithecus* also share with those of modern *Homo* a more symmetric crown, the absence of an anterior triangular face of the UP1, and a shallow mesiodistal groove between premolar cusps (Wood and Engleman 1988). However, *Australopithecus* premolars retain a paracone intermediate in size between those of extant humans and chimpanzees, the shape of the UP2 in occlusal view retains the primitive oval shape, and the UP1 sometimes has a mesial beak as seen in nonhuman hominids (Harrison 2011). There is also some evidence of even more root reduction; most *Australopithecus* UP1s have only two roots (Wood and Abbott 1988). The crowns of *Australopithecus* lower premolars retain an asymmetrical outline, though this is less pronounced than in nonhuman hominids. As in the upper premolars, there is some evidence of root reduction: the LP1 often has a Tome' root rather than a bifurcated root (Wood and Abbott 1988).

In the past, some researchers argued the *Australopithecus* dentition represents the primitive condition for the hominin clade (White et al. 1981). The *Australopithecus* postcanine dentition does retain some hominid symplesiomorphies and a few traits that we suggest may be primitive for the hominin clade; however, the overall postcanine morphology suggests a change from the generalized hominine dentition to more modern human-like crown and root morphologies.

Some researchers argue that *Kenyanthropus platyops* should be included in the genus *Australopithecus*, but its discoverers made a compelling case that it represents a separate early hominin genus (Leakey et al. 2001). *Kenyanthropus platyops* is known from a few specimens found in Kenya dating to ca. 3.5 Ma. Very few teeth are well-preserved in the hypodigm, but the type specimen features an *Australopithecus*-like dentition with well-developed protostylids and a primitive premolar root form. However, the UM1s and UM2s are much reduced in size. If the mandible KNM-WT 8556, currently referred to *Au. afarensis*, is found to represent *K. platyops*, then this taxon would also feature a large LM3 within the range of *Paranthropus,* and a well-developed LP2 talonid (Leakey et al. 2001); yet, this evidence would not fit with that from the cranium. Without additional specimens, however, it is difficult to reconstruct the characteristics and phylogenetic relationships of *Kenyanthropus*.

Paranthropus, for some a separate hominin subclade known informally as the "robust australopiths," is thought to have emerged in East Africa ca. 2.7 Ma. *Paranthropus* includes three species, two from East Africa (*Paranthropus boisei* and its likely ancestor, *Paranthropus aethiopicus*) and one from southern Africa (*Paranthropus robustus*). The derived masticatory morphology includes very large postcanine crowns, with thick enamel and an increased frequency of accessory cusps, especially on the mandibular teeth. Many upper molars have a lingual cingulum, and C6s are common on the lower molars; a C7 may also be present on the lower molars, but usually in combination with a C6 (Wood et al. 1983). Like those of *Australopithecus*, *Paranthropus* molars increase in size from mesial to distal, but the size gradient is more pronounced in the latter. Upper and lower premolars of *Paranthropus* are often molariform, and subsequently their crowns are more symmetrical than in other hominines. The lower premolars have greatly expanded talonids and almost always have more than two main cusps. Lower premolars often have three roots, a condition not shared with *Australopithecus* or *Homo*; it is likely secondarily derived from the ancestral condition of hominines, which features two-rooted lower premolars (Wood and Abbott 1988). Although similar to those of *Australopithecus* and *Homo* in some ways, the postcanine teeth of *Paranthropus* reflect a highly derived condition unlikely to be found in the basal hominin (Bailey and Wood 2007).

Many of the inferred derived postcanine macromorphological traits of modern humans can be found in earlier representatives of *Homo*, but these fossil taxa lack the pronounced postcanine reduction observed in modern humans. Some critical differences, however, exist between modern humans and the earliest proposed members of our genus. *Homo habilis* and *Homo rudolfensis* (some researchers refer these species to *Australopithecus* on the basis of their cranial morphology and primitive body form; see Wood and

Collard 1999) are sampled in East African deposits dating to just less than ca. 2 Ma; some claim *Homo habilis* may also be present in southern Africa at this time (Hughes and Tobias 1977; Curnoe and Tobias 2006). Unlike in modern *Homo*, the teeth of these taxa retain some primitive traits such as an apelike pattern of molar reduction where the M2 is the largest postcanine tooth of both upper and lower dentitions, a talonid basin that is expanded compared to that of later *Homo*, and lower premolars with two roots. In particular, *H. rudolfensis* retains larger postcanine crowns with more complex macromorphology than those of *H. habilis* (Wood 1991). *Homo rudolfensis* retains the primitive condition of a well-defined premolar buccal groove and bifurcated premolar roots. Early *Homo* provides corroborating evidence that some derived traits of modern human postcanine teeth, especially small crown size and reduction in root number, emerged relatively late in human evolution. Unless examples of reversions, they likely do not represent the primitive condition for the hominin clade.

The reduction of molar crown size and postcanine root complexity in *Australopithecus* and other fossil hominins suggests that these are traits that might be found in the MRCA of hominins and panins. The oval shape of the UP2 crowns of chimpanzees/bonobos and fossil hominins contrasts with the squarer shape of those in modern humans; the larger paracone of *Australopithecus* upper premolars suggests that paracone reduction did not occur in the human lineage until late in its evolutionary history. A large paracone is likely to have been the primitive condition of both hominins and panins.

It is possible that the postcanine teeth of the MRCA of hominins and panins may have been relatively large-crowned with thick enamel. This hypothesis contrasts with previous hypothetical reconstructions of the postcanine macromorphology of the MRCA suggesting small-crowned teeth with thin enamel (Pilbeam 1996). The principle of parsimomy suggests that the small size of postcanine tooth crowns of modern humans is derived; immediate precursors of the hominins likely had postcanine teeth similar in size to those of modern chimpanzees/bonobos. Most fossil hominines and hominins (other than *Paranthropus*) have thick enamel, although not as thick as in modern humans. Chimpanzees, sometimes described as having thin enamel, are more accurately described as having enamel that is intermediate in thickness or thicker than previously described (Shellis et al. 2008); some authors have described the enamel of chimpanzees as thick (Kono 2004). It is likely that the common ancestor of humans and chimpanzees/bonobos, and perhaps hominines more generally, had thick enamel relative to that of other primates. The somewhat thinner enamel of chimpanzees and distinctly thin enamel of gorillas is therefore most parsimoniously described as derived in these extant species; *Paranthropus* and *Homo* are derived in the opposite direction.

8.4.5 Postcanine morphology of stem taxa within the hominines

Thus far, we have focused on the likely primitive postcanine macromorphology of hominines and, more specifically, the likely primitive traits of the ancestor of hominins and panins. As the ancestral population subdivided, derived traits presumably began to accumulate within each subpopulation. Each of the three extant hominine genera (i.e., *Homo*, *Pan*, and *Gorilla*) has its own derived version of the primitive hominine postcanine macromorphology.

Although evidence from other parts of the Tree of Life suggests there would have been many more hominine and hominin clades than those represented by extant species (Figure 8.3), we can make more reliable predictions about clades with living members. In the next section we present predictions about the stem taxon in the gorilla clade, the chimpanzee/bonobo clade, and the human clade.

Gorillas are primarily folivores, and their postcanine teeth have taller shearing crests and thinner enamel than those of other extant hominids. Gorillas are also much larger, and some dental traits may relate to body size. Hypocones do not reduce to the same degree as in other hominids, and lingual cingula are common in the upper molars and premolars. The lower molars have especially large talonid basins, with a uniquely wide and deep separation between the

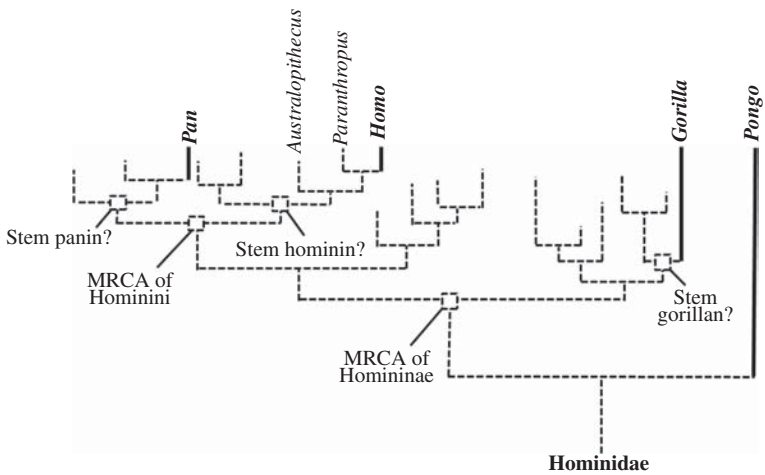

Figure 8.3. Hypothetical tree of extant hominines and fossil hominins demonstrating the potential adaptive diversity of the hominines through time. Solid lines indicate extant species, and dotted lines indicate hypothetical relationships between known and unknown fossil species. Open boxes indicate key fossils' relatives such as ancestors and stem taxa in reference to their modern relatives.

metaconid and entoconid. Lower molars often have buccal cingulids and the highest frequencies of extra cusps among extant hominids. In the lower premolars, a well-defined mesiodistal groove separates the paracone and protocone, and there are often buccal cingulids on the LP2s. Gorilla postcanine roots follow the general hominid pattern, but the upper premolars of some individuals have only two roots (Kupczik 2009).

We predict that the postcanine teeth of the stem gorilla will be large, featuring extensive talonid basins and large paracones. The postcanines, like those of modern gorillas, will feature higher relief than the intermediate relief proposed for the MRCA of hominines. Additional cusps on the premolars, wide and deep separation between postcanine cusps, and lingual cingula and buccal cingulids may also be diagnostic.

Although chimpanzees/bonobos and gorillas are closely related and some have argued that they represent allometric versions of the same body plan (Hartwig-Scherer 1993; Gunz 2012), their postcanine macromorphology is independently derived. The species of chimpanzee and bonobo are smaller than other great apes, and, as in modern humans, there is relatively little sexual dimorphism. Chimpanzees and bonobos have lower levels of both inter- and intraspecific occlusal postcanine variation than observed in gorillas and orangutans (Pilbrow 2003); with respect to upper molars their hypocones are notably reduced from M1 to M2, the distolingual groove is not distinct, and extra cusps are rare. As is the case for gorillas, lingual cingula are common on chimpanzees and bonobo upper molars, especially on the mesial teeth; uniquely among extant hominids, chimpanzee and bonobo upper molars often have buccal cingula, although these are seldom prominent. The lower molars have high rates of variation in the Y-5 pattern, and there is often agenesis of the distal main cusp, especially in LM3. The mesial fovea (i.e., occlusal basin) of lower molars is extensive, and the cusps are in consequence pushed to the crown margins. Unlike other great apes, in which the M2 is usually the largest postcanine tooth, chimpanzees and bonobos more often share with modern humans a distal reduction pattern in the upper molars in which UM2 is intermediate between a larger UM1 and smaller UM3 (Mahler 1980).

The premolars of chimpanzees and bonobos follow the general hominid pattern, with a notable exception being the absence of cingula. Variation in premolar root number is common, especially among females. The latter sometimes possess LM1s with a single root and fused double root, and a least one male is known to have a double-rooted UP2 (Abbott 1984; Kupczik 2009). Some have reported that enamel thickness is intermediate between that of *Pongo* and gorillas (Shellis et al. 1998), while others described *Pan* as having thin (Schwartz 2000; Nagatoshi 1990) or thick (Kono 2004) enamel. We predict that although the MRCA of hominines may have had peripherally located cusps, expression of this

trait along with its corollary, an expanded mesial fovea, will be more pronounced in the stem panin. Buccal and lingual cingula may be common on molars, as in modern chimpanzees and bonobos, and there may be some reduction in enamel thickness relative to that of the MRCA of hominins and panins.

As in other extant hominines, the modern human dentition is derived. Modern humans have the smallest postcanine teeth of any hominid; reduction or agenesis of the upper and lower M3s is common. In the upper molars, a lingual cingulum is present in some populations and is referred to as Carabelli's cusp (Turner and Hawkey 1998). In the lower molars, modern humans share with chimpanzees and bonobos reduced hypoconulids, and their distal molars often have fewer than five cusps. Unlike in other hominids, upper premolars of modern humans are trapezoidal rather than square and have prominent buccal cusps. The LP1 is nonsectorial, lacking any evidence of a honing complex; it is oval like the LP2 and often bicuspid with a prominent metaconid. Unlike other hominids, modern humans usually have single-rooted premolars, although the UP1s may be double-rooted. Compared to other primates and hominines, modern humans have hyperthick enamel.

Comparisons with other fossil hominins, particularly early members of the *Homo* lineage, suggest that most of these hypothesized derived characteristics of modern humans evolved relatively late in human evolution and may relate to the use of cooking and other food processing (Wrangham and Conklin-Brittain 2003). Postcanine macromorphological traits of the earliest hominins may include an increase in relative enamel thickness, cusps that are more centrally located on crowns, and either a reduced or an absent LP1 honing facet. Postcanine roots of the earliest hominins may show evidence of reduction.

8.4.6 Assessment of the postcanine macromorphology of possible hominins

Most current estimates suggest that the MRCA of hominins and panins likely evolved between 7 and 5 Ma (Kumar et al. 2005), but new estimates based on generation times have pushed this date further back (Langergraber et al. 2012). A global expansion of C_4 grasses occurred 8–7 Ma (Harrison 2010), forcing Eurasian hominoids into refugia in southeastern Asia and Indonesia – to separate them from African hominoids; these African populations likely included ancestors of the hominines. Between 7 and 5 Ma, Africa became cooler and drier, open environments expanded, and forests fragmented (deMenocal and Bloemendal 1995). The emergence of mosaic environments may have led to speciation among the African hominoids (Richmond et al. 2001). Several hominine

taxa are known from in and around the 7 and 5 Ma interval, and different groups of researchers have argued that each of them was an early hominin.

Sahelanthropus tchadensis, the oldest of these purported hominin taxa, is known from ca. 7 Ma deposits in Chad. The well-preserved but distorted cranium and jaw fragments include some postcanine teeth that are intermediate in size between those of chimpanzees and modern humans; the enamel thickness has been described as intermediate between those of these clades (Brunet et al. 2002). Lower premolars of *Sahelanthropus* share with both early hominins and chimpanzees a weakly expressed mesial beak, and an expanded talonid with later hominins and some hominines. The postcanine roots are not noticeably reduced in form or number. Thus, *Sahelanthropus* lacks some of the key derived traits we predict in the MRCA of hominins and panins and in the stem hominin taxon. It is possible that *Sahelanthropus* is a hominin, but on the basis of its postcanine macromorphology, we think it is more prudent to consider it a hominine, tribe *incertae sedis*.

Orrorin tugensis is known from fossils recovered from ca. 6 Ma sediments exposed in the Tugen Hills, Kenya. Compared with the fossil record of other possible early hominins *Orrorin* has an unusually high concentration of postcranial fragments; only a few tooth crowns can be reliably attributed to this taxon. The postcanine teeth are small, within the range of modern *Homo*, with thick enamel and relatively centrally located cusp tips; the UM3 is reduced, but its triangular shape is unusual (Senut et al. 2001). As in chimpanzees and other apes, the upper molars have distal foveae. It is not parsimonious for the MRCA of *Homo* and *Pan* to have small teeth that only increase again in both lineages; it is therefore unlikely that *Orrorin* represents the MRCA of hominins and panins. We do not exclude *Orrorin* as a possible stem hominin, but on the basis of what little we know of its postcanine macromorphology, and in the absence of evidence about root morphology, we think it is best to be conservative and consider it as a hominine, tribe *incertae sedis.*

The genus *Ardipithecus* presently comprises two species, both found in Ethiopia. *Ardipithecus ramidus* is represented by several individuals, one of them an unusually complete associated skeleton dating to ca. 4.4 Ma. The fossil record for *Ardipithecus kadabba* is sparser and considerably older (5.8–5.2 Ma). The postcanine macromorphology of *Ardipithecus* includes relatively small, broad teeth with enamel thickness intermediate between those of modern humans and chimpanzees and relatively centrally located main cusps (Suwa et al. 2009; White et al. 1994).

The lower dentition features metaconids that are shifted mesially, as is the case in *Australopithecus*. Lower premolars have a mesial beak and large talonid and are intermediate in their degree of symmetry between those of humans and chimpanzees/bonobos. The UP1 has a triangular portion as in apes and higher

asymmetry than in most hominins, but the upper molars lack well-expressed anterior foveae and feature weak distolingual grooves like those in *Homo*. It is difficult to assess whether a honing facet is present on the LP1 of *Ardipithecus*. In the announcement of *Ar. kadabba*, a honing facet is described as a general trait of the genus (Haile-Selassie 2001). However, in subsequent descriptions of the *Ar. ramidus* dentition, there is no reference to a honing facet.

Traits of the postcanine macromorphology of *Ardipithecus* are consistent with its being a member of a closely related extinct clade, but there is no evidence of the larger postcanines, reduced complexity in the crown of the upper and lower M3, or reduction in root number that we predict would be the case for the stem hominin. The presence of a honing facet in *Ar. kadabba* almost certainly excludes that taxon from being a hominin. If *Ar. ramidus* is a stem hominin, its geological age is inconsistent with recent molecular predictions for the date of divergence between hominins and panins (Langergraber et al. 2012).

Applying the hypotheses that we have generated about the postcanine macromorphology of the ancestral morphotypes and stem taxa of the extant hominine lineages, we find it more appropriate to assign the taxa others consider to be the earliest hominin to hominines more generally; *Ar. ramidus* possibly belongs to an extinct clade closely-related to humans and chimpanzees/bonobos. No matter what taxonomic hypothesis is applied to these taxa, all involve the acceptance of homoplasy either within, or beyond, the hominin clade; in the case of some hypotheses, homoplasy is likely both within and beyond the hominin clade. This possibility is not unexpected, for it reflects a general trend in many mammalian lineages to diversify through successive adaptive radiations of which only a few species survive (Wood and Harrison 2011). Such events are well-accepted within other mammalian lineages, including the orangutan, but researchers seem more hesitant to accept this "messy" view of evolution within hominines and hominins (Begun 2004).

It is reasonable to assume that many more hominines have existed than the species that are extant (i.e., modern humans, chimpanzees, bonobos, and gorillas). There are just four genera of extant hominids (i.e., those listed plus *Pongo*), but at least twenty-four other hominid genera are known from fossil deposits in Europe, Asia, and Africa spanning more than 18 million years. Many species within these genera have been interpreted at one time or another as hominins, even though modern humans represent less than 15 percent of extant hominid diversity. The propensity of paleoanthropologists to refer late Miocene hominines from Africa to the hominin clade likely inflates our interpretation of early hominin diversity (Andrews and Harrison 2005; Begun 2004; Harrison 2010). Fossil taxa currently proposed as early hominins may represent stem hominins or the MRCA of hominins and panins, but they are just as likely, if not more likely, to represent sister taxa of the hominins or the MRCA (Wood 2010).

8.5 Conclusion

We used nonmetric traits to review the postcanine macromorphology of extant and fossil hominines, plus their closest extant hominid relative, *Pongo*. From the distribution of these traits we propose the following predictions for the postcanine macromorphology of key – and likely yet to be discovered – taxa within the hominine lineage:

1. *Most recent common ancestor of hominines*: The postcanines of this taxon will feature traits shared among all hominids, including relatively large, elongated crowns; a Y-5 cusp pattern in the lower molars; well-developed talonids on molars and premolars; lower premolars with three foveae; and an LP1 with evidence of a honing facet. The postcanine crowns may also have greater crown relief than *Pongo* and more peripherally located cusps.
2. *Most recent common ancestor of hominins and panins*: The postcanines of this taxon will be homininelike but with a reduction in the complexity of molar crowns and roots of all postcanine teeth. The upper and lower M3s may be smaller, but otherwise there will be no significant decrease in overall postcanine size compared to that in other hominines. The teeth may have thicker enamel than that of other hominines, and the honing facet may be more weakly expressed. Roots of the postcanines, especially premolars, may show some evidence of root reduction.
3. *Stem taxon of the gorilla clade*: The postcanines of this taxon will be hominine-like, but the crowns will be larger with expanded talonids and larger paracones. Crowns will also feature high cusp relief, additional cusps may be present on the premolars, there will be wide and deep separation between buccal and lingual cusps, and lingual cingula and buccal cingulids may be common.
4. *Stem taxon of the chimpanzee/bonobo clade*: Postcanines of this taxon (i.e., stem panin) will be similar to those of the MRCA of hominins and panins, but they will have more peripherally located cusps, and thus an expanded mesial fovea. Buccal and lingual cingula may be present on the molars, and there may be some reduction in enamel thickness.
5. *Stem taxon of the human clade*: The postcanines of this taxon (i.e., stem hominin) will be similar to those of the MRCA of hominins and panins, with the addition of an increase in relative enamel thickness, more centrally-located cusps, and a reduced or absent honing facet.

These are hypotheses, not definite statements about the postcanine macromorphology of the two MRCAs and the stem taxa of the extant hominine clades. Recent fossil discoveries (e.g., *Ar. ramidus*, *Au. sediba*, Red Deer Cave

people) serve to remind us that extant taxa and the better known extinct taxa do not exhaust the possible combinations of primitive and derived morphologies.

Before decisions are made about the taxonomy and phylogenetic relationships of newly discovered fossils that are interpreted as providing evidence of a hitherto unknown taxon, the morphology of each region should be compared with predictions such as those set out previously for the macromorphology of the postcanine tooth row. The fossil evidence we have almost certainly represents a small percentage of the taxa that have ever lived; we are much more likely to discover closely-related taxa of extant species than their direct ancestors. Using hypotheses of primitive and derived traits of ancestral populations allows us to test the likely phylogenetic relationships of these closely related taxa.

No doubt as we add more information from new fossil finds and new studies of developmental plasticity, these hypotheses will continue to be improved. Developmental studies have proved to be particularly promising in reconstructing the potential evolutionary pathways of postcanine macromorphological traits. Comparable studies of enamel formation have demonstrated that the hyperthick enamel of *Paranthropus* and modern *Homo* is achieved through different patterns and is therefore possibly homoplasic (Beynon and Dean 1988; Wood 2010). Similarly, developmental modeling of cusp patterning indicates that accessory cusps in the lower molars may be a result of a general increase in tooth size (Skinner and Gunz 2010). There is a pressing need for more comparative studies of premolar morphology and postcanine root morphology, for there is evidence that these structures have particular valency with respect to the alpha taxonomy and phylogenetic relationships within and around the hominin clade. Studies of postcanine development in juveniles may also aid in our assessment of the polarity of key dental traits and may be especially important in the wake of new evolutionary developmental studies of mammalian dental development.

We hope this review will inspire such studies and encourage others to challenge and refine our working hypotheses concerning the probable postcanine macromorphology of the ancestral morphotype and the stem taxa within the hominine clade. Such predictive frameworks will help evaluate the taxonomy and phylogeny of future fossil discoveries, especially those that are claimed to be ancestors or early representatives of the hominin clade.

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9 *Dental morphology of European Middle Pleistocene populations*

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9.1 Introduction

The origin of Neanderthals has been classically explained by the gradual accumulation of so-called Neanderthal features until the appearance of classic Neanderthals in the Upper Pleistocene; this process has been termed the "accretion model" (Hublin 1996). Hard glacial conditions and climatic instability during the Middle Pleistocene would have implied frequent bottlenecks and local extinctions with subsequent fixation of the Neanderthal traits by genetic drift and a decrease in morphological variability (Hublin 1998; Maureille and Houët 1998; Trinkaus 1983, 1993). Along these lines, previous studies have suggested that Neanderthals exhibit a unique dental morphological pattern among hominins (e.g., Bailey 2002a; Bailey and Lynch 2005; Bailey et al. 2011; Bermúdez de Castro 1993; Gómez-Robles et al. 2007, 2008; Martinón-Torres et al. 2007a, b). However, approaches to studying this "uniqueness" and the evolutionary weight of these traits requires a concomitant analysis of dental morphology in European Middle Pleistocene populations considered ancestral to the Neanderthal lineage (Arsuaga et al. 1993, 1997a; Hublin 1982, 1984, 1996, 2009; Martínez and Arsuaga 1997; Stringer 1985, 1993).

To date, the Sima de los Huesos (SH) site (Burgos, Spain) has provided the largest Middle Pleistocene hominin collection world-wide, with more than

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5000 fossils representing all skeletal elements and an MNI of 28 individuals (Bermúdez de Castro et al. 2004a, b, c). Dated to 400,000–500,000 BP (Bischoff et al. 2003, 2007), this hypodigm provides possibly the earliest example of a hominin population with Neanderthal features. In addition, it provides an unparalleled opportunity to study intrapopulation variability (e.g., Arsuaga et al. 1997b; Gómez-Olivencia 2009; Gómez-Olivencia et al. 2007; Gómez-Robles et al. 2007, 2008, 2011a, b; Lorenzo et al. 1998; Martinón-Torres et al. 2006). A recent study that compared the Sima de los Huesos dental sample against *H. neanderthalensis*, *H. sapiens,* and the European Middle Pleistocene populations revealed that SH fossils present all morphological traits that are usually considered typical of *H. neanderthalensis* either in their degree of expression, frequency, or a combination of the two (Martinón-Torres et al. 2012). In addition, they display some features that make the SH population more derived than other contemporaneous groups and some classic Neanderthals (Martinón-Torres et al. 2012). One of the main impediments to understanding the evolutionary story of the Neanderthal lineage is the scarce fossil record for the Middle Pleistocene, aside from the SH sample. Thus, it is not possible to know the true variability and degree of "neanderthalization" of *H. heidelbergensis* dentitions. Yet it is possible to explore variability of the SH specimens and assess whether they are Neanderthal-like "on average" and/or individually.

9.2 Materials and methods

The total dental sample from SH consists of 525 permanent teeth (236 maxillary, 289 mandibular). The detailed list of specimens is in Martinón-Torres et al. (2012). Observations were made mostly on originals or high-quality replicas. To assess the degree of "neanderthalization" of the SH sample, we compared it to other hominin fossils from the Middle Pleistocene of Europe (*H. heidelbergensis* [HEI]), a wide sample of *H. neanderthalensis* (NEA) and early *H. sapiens* (ESAP), and a contemporary *H. sapiens* sample (SAP) (Table 9.1). To explore the degree of "neanderthalizaton" of each SH individual, we calculated distances on a pairwise basis with individuals from the same hominin comparative samples.

Analysis was based on the frequency of expression of relevant traits for upper incisors, lower first premolars, and upper third molars. We employed the Gower coefficient because it combines ordinal and nominal variables. We then performed a multidimensional scaling analysis, or MDS (PAST® software; Hammer et al. 2001), a data reduction technique that illustrates distances among individuals in a plot, like a map (Kruskal and Wish 1978), in which the proximity among samples illustrates levels of phenetic affinity. Finally,

Table 9.1. *Comparative dental sample*

***H. heidelbergensis* (HEI)**	Arago*; Mauer*; Mountmarin*; Pontnewydd; Steinheim.
***H. neanderthalensis* (NEA)**	Arcy-sur-Cure* (Renne, Hyène, Loup, Bison); La Quina 5; Malarnaud*; Petit-Puymoyen*; Pinilla del Valle (Madrid, Spain)*; Cabezo Gordo; Engis II; Fondo Cattíe; Saccopastore*; Tabun (Tabun C1*); Krapina; Le Moustier 1; Monsempron; Saint-Césaire; Shanidar; Sidrón (005,008).
Contemporary *H. sapiens* (SAP)	Hispanic-Muslim medieval collection of San Nicolás (Murcia, Spain)*; Mesolithic North African sample* (Afalou, Tebessa, Aïn Meterchem, Gambetta, Aïn Dokkara, Taforalt); Mesolithic French sample* (Téviec and Hoëdic); Neolithic French sample* (Avize, Dolmens de Bretons, Caverne de L'Homme Mort, Orrouy).
Fossil *H. sapiens* (FSAP)	Abri Pataud*; Dolní Věstonice*; St Germain de la Rivière*; Isturitz*; Pavlov*; Qafzeh*; Les Rois*; Espugo*; Almonda (Zilhão 1997); Caldeirão (Trinkaus et al. 2001); Predmostí; Brassempouy; Mladeč; El Wad; Skhul.

Notes: The *Homo heidelbergensis* denomination was employed to refer exclusively to the European Middle Pleistocene fossils.

* Observations were made on originals.

a convex hull was determined for each group (except for *H. heidelbergensis* where sample size was too small). The convex hull is the smallest convex polygon that includes all specimens in a sample and provides a graphic representation of the distribution of a given group for the traits studied. By exploring the MDS plot and convex hulls, we assess whether (1) the SH specimens fall within the distribution area of Neanderthals and (2) whether the variability of this Middle Pleistocene population is higher than that of *H. neanderthalensis*, as the accretion process would predict. Individuals with more than one missing value were not included. In some cases, the number of variables was reduced to maximize the number of individuals per hominin group, particularly in the case of the small *H. heidelbergensis* sample.

9.3 Results

Detailed pictures of the SH specimens and definitions and grade-scales of the morphological traits employed here can be found in Martinón-Torres et al. (2012). Figures 9.1 through 9.7 provide an illustration of a selected sample of SH upper and lower teeth.

Figure 9.8 provides the MDS plot and convex hulls for UI1 based on the expression of labial convexity, shoveling, and *tuberculum dentale*. There is

Figure 9.1. From left to right and upper to lower: AT-1472 (right LI1), AT-104 (left LI1), AT-1460 (left LI1), AT-275 (right LI1), AT-1469 (right LI1), AT-55 (right LI2), AT-597 (left LI2), AT-103 (left LI2), AT-167 (left LI2), AT-67 (left LC), AT-1952 (right LC), AT-1951 (right LC), AT-161 (left LC), AT-276 (left LC), AT-578 (left LC) from Sima de los Huesos. Illustrations: Eduardo Saiz.

Figure 9.2. From left to right and upper to lower: AT-2027 (right LP1), AT-47 (left LP1), AT-4100 (left LP1), AT-1760 (left LP1), AT-4328 (right LP1), AT-148 (right LP1), AT-221 (right LP2), AT-580 (left LP2), AT-603 (left LP2), AT-1465 (left LP2), AT-1763 (left LP2), AT-277 (right LP2). Illustrations: Eduardo Saiz.

some overlap of the SH and *H. neanderthalensis* samples on one hand and early and contemporary *H. sapiens* samples on the other. The early *H. sapiens* specimens fall mainly within the contemporary *H. sapiens* distribution, although some are within the range of variation for *H. neanderthalensis* and SH. There is no overlap of the modern human group with either *H. neanderthalensis* or the SH group. Most SH specimens fall inside the *H. neanderthalensis*

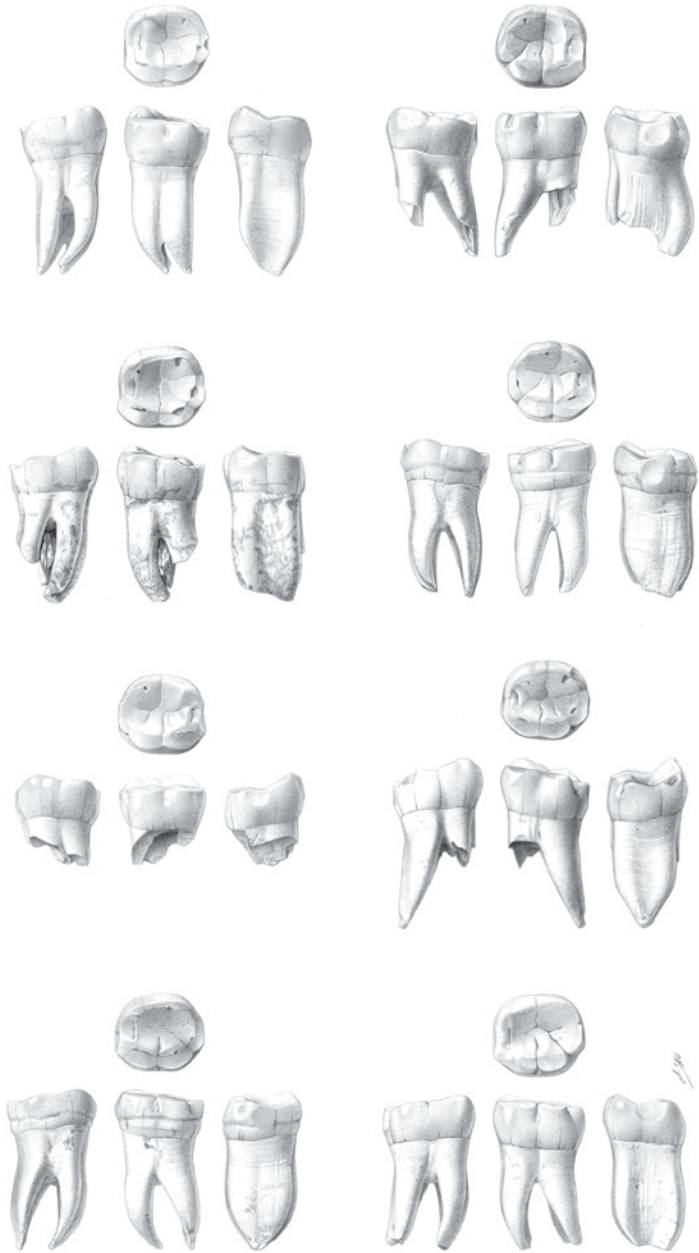

Figure 9.3. From left to right and upper to lower: AT-22 (left LM1), AT-2276 (right LM1), AT-1759 (left LM1), AT-141 (right LM1), AT-272 (right LM1), AT-286 (left LM1), AT-556 (left LM1), AT-1459 (left LM1). Illustrations: Eduardo Saiz.

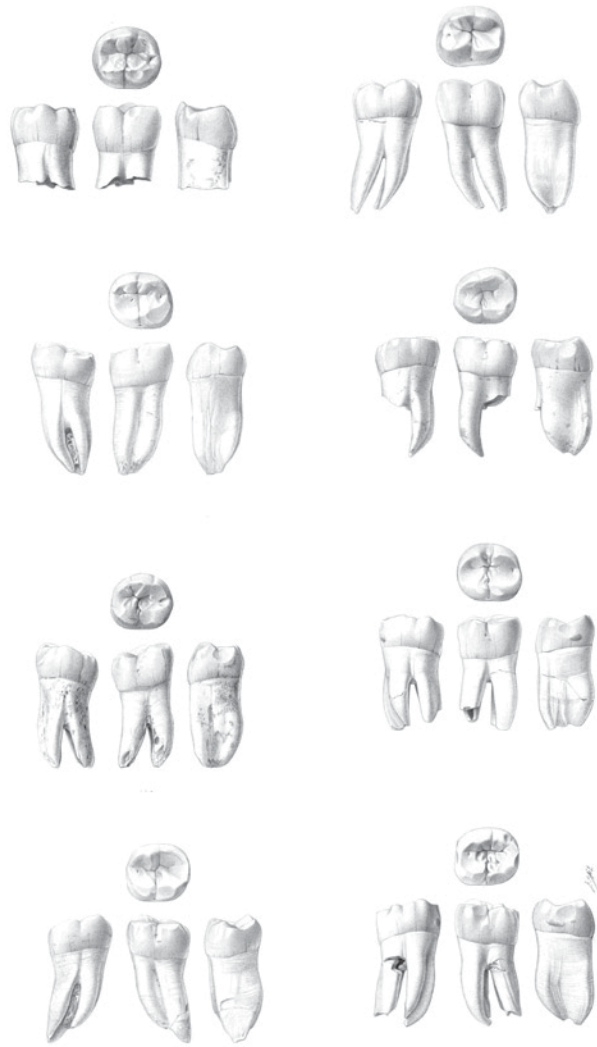

Figure 9.4. From left to right and upper to lower: AT-142 (right LM2), AT-3179 (left LM2), AT-271 (right LM2), AT-169 (left LM2), AT-1761 (right LM2), AT-284 (right LM2), AT-273 (left LM2), AT-2272 (left LM2). Illustrations: Eduardo Saiz.

convex hull except those which express milder forms of dental tubercles and shoveling. One *H. heidelbergensis* specimen is within the early and contemporary *H. sapiens* distributions, whereas the other falls outside of the four convex hulls and near *H. sapiens* and *H. neanderthalensis*. The location of the two

Figure 9.5. From left to right and upper to lower: AT-27 (left UI1), AT-42 (right UI1), AT-3885 (left UI1), AT-2279+AT-3197 (left UI2), AT-4334 (right UI2), AT-3016 (right UI2), AT-5621 (left UC), AT-1757 (lower UC), AT-1475 (right UC), AT-1758 (right UC), AT-1942 (left UC), AT-5616 (right UC). Illustrations: Eduardo Saiz.

Figure 9.6. From left to right and upper to lower: AT-813 (left UP1), AT-823 (right UP1), AT-41 (left UP1), AT-3186 (right UP1), AT-4325 (left UP1), AT-5611 (left UP1), AT-409 (left UP2), AT-68 (right UP2), AT-746 (right UP2). Illustrations: Eduardo Saiz.

H. heidelbergensis specimens should be interpreted with caution, since each has a missing value. However, Arago 111 suggests at least moderate labial curvature and a pronounced *tuberculum dentale* (i.e., close to the pattern of *H. neanderthalensis,* SH, and a few exceptions of the modern group), whereas Arago 61 does not possess a *tuberculum dentale* and displays a less developed shovel shape – to cluster with *H. sapiens*.

The MDS for UI2 morphology (Figure 9.8) is based on the expression of labial convexity, shoveling, and *tuberculum dentale*. As with UI1, there is an

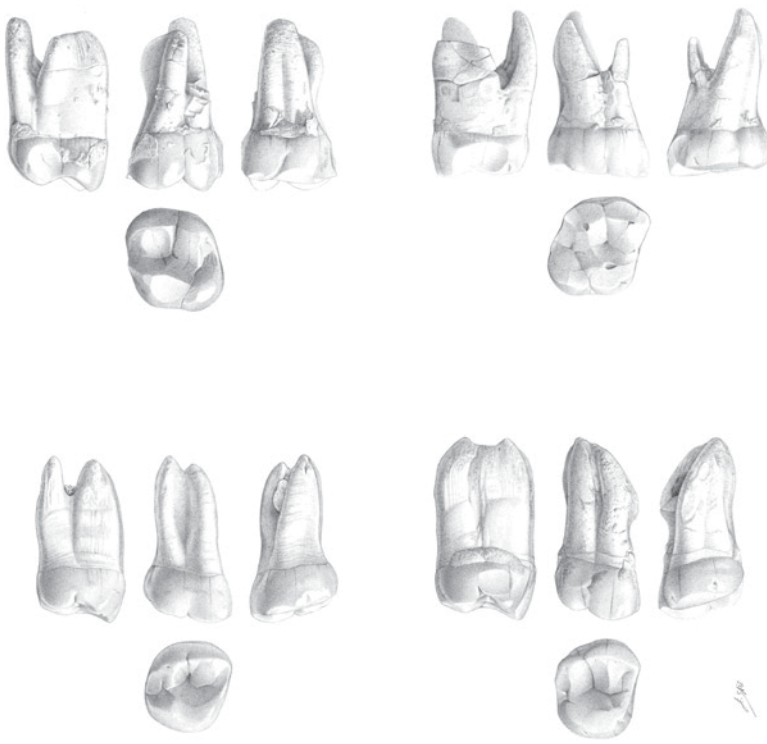

Figure 9.7. From left to right and upper to lower: AT-3177 (left UM1), AT-20 (right UM1), AT-817 (right UM2), AT-822 (right UM2). Illustrations: Eduardo Saiz.

overlap of SH and *H. neanderthalensis* on the one hand and early and modern *H. sapiens* on the other. One difference is the lack of overlap between the convex hulls of SH and Neanderthals with that of early and modern *H. sapiens*. One *H. heidelbergensis* specimen falls outside the convex hull of the four groups; the other is within the distribution of early *H. sapiens*. These teeth would be "less Neanderthal" than the SH specimens because both lack a *tuberculum dentale* and one presents a less pronounced shovel shape than is common in Neanderthals. The few SH specimens that fall outside the range of *H. neanderthalensis* variation are also those without an obvious *tuberculum dentale*. However, in those cases, identification of the trait may be obscured because it is merged with pronounced marginal ridges (Martinón-Torres et al. 2007b, 2012).

Figure 9.9 provides the MDS for the UC morphological comparison; it is based on the expression of shoveling, *tuberculum dentale*, and canine mesial

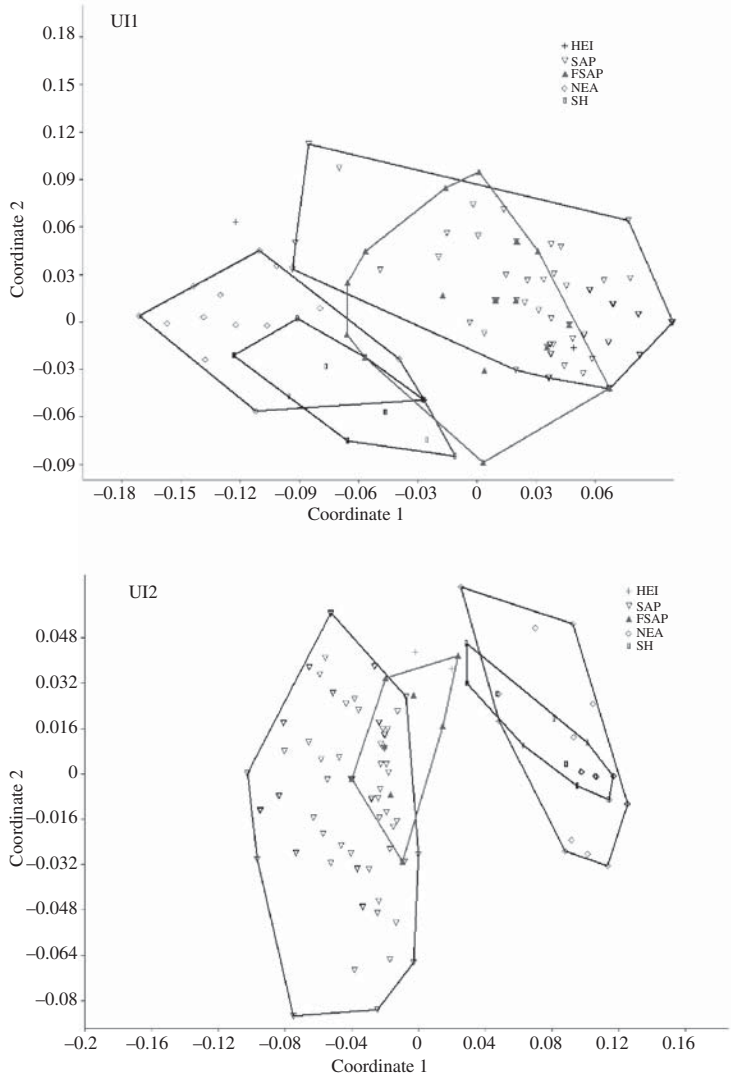

Figure 9.8. Multidimensional scaling plots and convex hulls of *H. heidelbergensis* (HEI), modern *H. sapiens* (SAP), fossil *H. sapiens* (FSAP), *H. neanderthalensis* (NEA) and Sima de los Huesos (SH) groups for UI1 (upper) and UI2 (lower).

ridge. Again, there is some overlap of early and modern *H. sapiens* samples on one side and SH and *H. neanderthalensis* on the other. The *H. heidelbergensis* specimens fall within the convex hulls of SH and Neanderthals. There is slight overlap among the four main groups, although there is a tendency for SH and

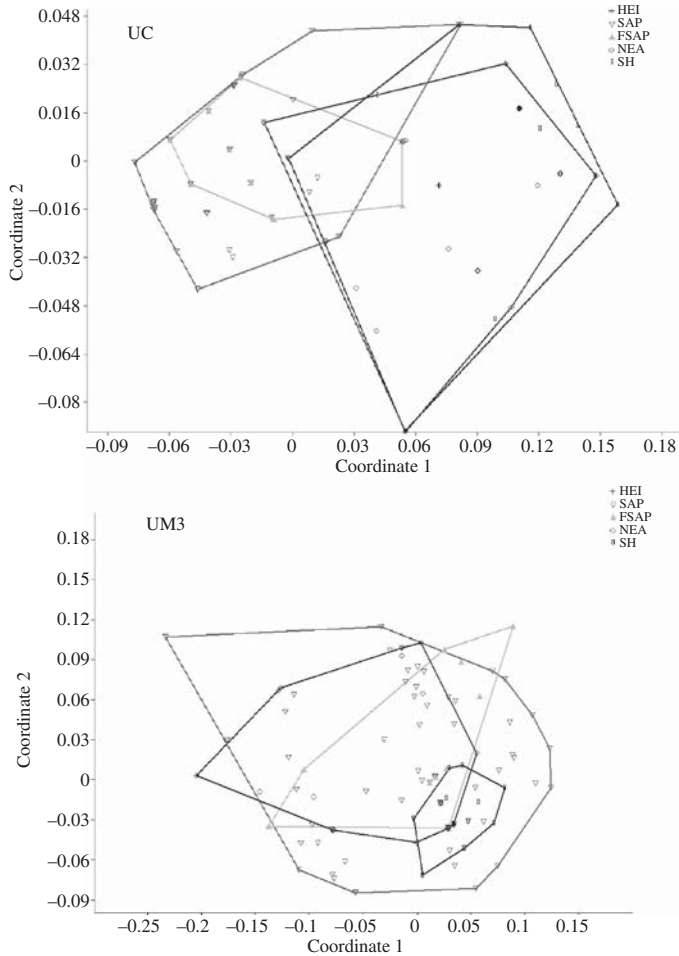

Figure 9.9. Multidimensional scaling plots and convex hulls of *H. heidelbergensis* (HEI), modern *H. sapiens* (SAP), fossil *H. sapiens* (FSAP), *H. neanderthalensis* (NEA) and Sima de los Huesos (SH) groups for UC (upper) and UM3 (lower).

Neanderthal specimens to cluster on the positive side of the x-axis; the *H. sapiens* groups tend to cluster toward negative values. Although most SH specimens are within the range of Neanderthal variation, some fall outside toward the positive values of the x-axis, thus evincing their *extreme* position along the Neanderthal spectrum. Neanderthal and SH specimens tend to show high frequencies of shoveling, *tuberculum dentale*, and canine mesial ridge expression relative to these traits in *H. sapiens* groups.

Figure 9.9 illustrates the MDS for comparison of the UM3 in five groups and is based on grades of expression for the metacone, hypocone, C5, and *crista obliqua*. For this tooth class, there is a general overlap of the four distributions and the *H. heidelbergensis* specimens. Modern *H. sapiens* almost covers the variability of all the other groups, except for one Neanderthal specimen and three early *H. sapiens* specimens. The SH convex hull is small and illustrates the low variability of this population for UM3; it overlaps with all groups, but particularly with modern *H. sapiens* in a region where no other specimens of the other populations fall. The clustering of these SH specimens with modern humans is due to the strong dental reduction of the SH molars, which fits within the range of variation of modern *H. sapiens.*

Figure 9.10 represents the MDS plot for the comparison of LP2 morphology and is based on the number of accessory lingual cusps, position of the metacone and the expression of the transverse crest, and the mesial and distal accessory ridges of the protoconid. For this tooth class, modern *H. sapiens* shows the greatest variability, almost covering the distribution of all other specimens from the remaining groups. *H. heidelbergensis* specimens fall within the SH convex hull and the latter fits within the *H. neanderthalensis* distribution, which shows higher variability than the SH group. The early *H. sapiens* sample is also contained within modern *H. sapiens*, and presents a zone of overlap with SH and *H. neanderthalensis*, but not with *H. heidelbergensis*. Thus, *H. sapiens* presents some conformations that are exclusive to this species and also cover the typical morphologies found in SH, *H. heidelbergensis* and *H. neanderthalensis*. SH intrapopulational variability would be lower than that of the Neanderthal group.

The MDS plot for the UM2 comparison, illustrated in Figure 9.10, is computed using the anterior fovea, mid-trigonid crest, distal trigonid crest, deflecting wrinkle, groove pattern and degree of expression of the hypoconulid, C6, and C7. All SH specimens fall within the *H. neanderthalensis* convex hull and, with one exception, the SH group does not overlap with modern *H. sapiens*. There is an area of exclusive overlap between both *H. sapiens* groups along the positive end of the x-axis, but there is an area of general overlap among Neanderthals, SH, *H. heidelbergensis,* and early *H. sapiens*. *H. heidelbergensis* shows higher variability than the SH group, with specimens falling outside any convex hull in the *H. sapiens* groups' area and in the *H. heidelbergensis* and Neanderthals' zone.

9.4 Discussion

This study provides a further exploration of the Sima de los Huesos dental morphology relative to Neanderthals, *H. sapiens,* and other Middle Pleistocene

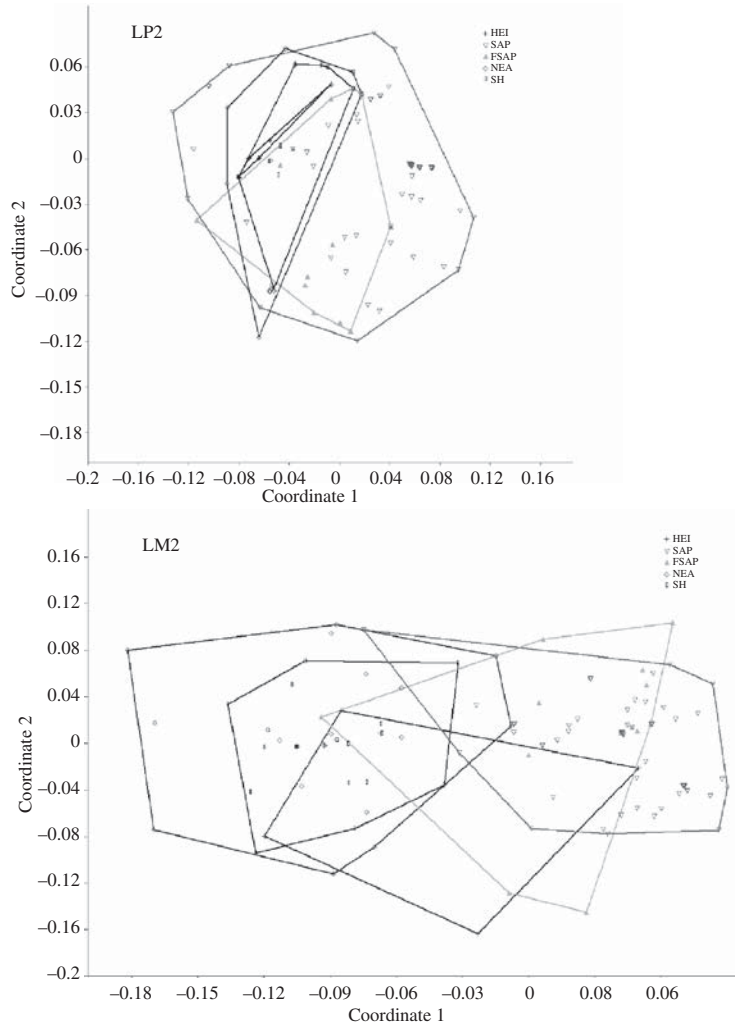

Figure 9.10. Multidimensional scaling plots and convex hulls of *H. heidelbergensis* (HEI), modern *H. sapiens* (SAP), fossil *H. sapiens* (FSAP), *H. neanderthalensis* (NEA) and Sima de los Huesos (SH) groups for LP2 (upper) and UM2 (lower).

groups. The results support previous conclusions about the morphological pattern of this population, ratifying the expression of typically Neanderthal conformations (Bermúdez de Castro 1986, 1988, 1993) but also some features that are apparently more derived than those identified in other contemporaneous and even later groups (Martinón-Torres et al. 2012).

The SH UI1 and UI2 appear Neanderthal-like by displaying high frequencies of pronounced labial convexity, shoveling, and *tuberculum dentale*. In particular, the UI1s present a "triangular shovel shape" (Martinón-Torres et al. 2007a, b); in this case, thickened and massive marginal ridges invade the lingual aspect and define a deep longitudinal fossa. The combination of lingual morphology together with strong labial convexity provides these teeth with a typical "triangular" or "V-shape" in occlusal view. This morphology has been described as typical of European Middle Pleistocene groups and *H. neanderthalensis* (de Lumley 1973; Martinón-Torres et al. 2007a, b) and can be traced back in milder forms to Early Pleistocene groups from Europe and Asia (Martinón-Torres et al. 2007a, b). The SH specimens show a greater overlap with *H. neanderthalensis* than *H. heidelbergensis*, which fall outside Neanderthal variation in both the UI1 and UI2 analyses (Figure 9.8). Expression of milder forms of shoveling and *tuberculum dentale* in the SH UI1 (but not SH UI2) would probably be one of the few traits where this population shows less pronounced forms than in *H. neanderthalensis* (Bailey 2002a; Crummett 1994; Mizoguchi 1985). For the remaining traits, SH specimens are "as Neanderthal" as *H. neanderthalensis* or more so, occupying *extreme* positions along the Neanderthal spectrum of variation. One example is evident in the UC analysis (Figure 9.9) where SH overlaps Neanderthals in their expression of *mass-additive* traits (term from Irish 1998). Like many other dental and skeletal features, these traits are polymorphic – which would explain the areas of overlap with *H. sapiens*. However, there is also an area occupied exclusively by Neanderthals, SH, and *H. heidelbergensis*, and an area to the right of the Neanderthal spectrum on the x-axis, where only SH specimens are found. From all dental classes studied here, this would be the only case where the SH distribution is larger than that of the Neanderthal; paradoxically, the SH spectrum covers morphologies more pronounced than in the Neanderthal group itself. The UM3 comparison shows that actual *H. sapiens* populations cover all morphologies seen in the earlier groups (Figure 9.9), but within those morphologies some expressions are typical of Neanderthals, *H. heidelbergensis* and SH. Interestingly, there are forms that are exclusively shared between modern *H. sapiens* and SH. They are related to the strong dental reduction ascertained in the SH populations (Bermúdez de Castro 1987; Bermúdez de Castro and Nicolás 1995), to an exceptional degree for Middle Pleistocene populations and Neanderthals, and within the range of variation of modern groups. Future studies should further explore whether this reduction evinces a higher derived stage in SH population compared to other groups, or whether it represents an intra-group peculiarity. In both cases, the SH sample would not fit the progressive neanderthalization processes hypothesized with the accretion model (Hublin 1996); the SH group shows more derived forms than approximately

contemporaneous or even later hominin populations. In addition, the small convex hull of the SH group for the UM3 means that variability for this tooth class is clearly smaller than that of the Neanderthal species.

Although we have the handicap of not knowing the true variability of Middle Pleistocene European populations given the scarce fossil record (aside from SH), and we do not know if the SH sample is representative of European Pleistocene groups, the SH hypodigm would not support the expected decrease in morphological variability along the Neanderthal lineage as hypothesized by the accretion model (Hublin 1998; Maureille and Houët 1998; Trinkaus 1983, 1993). Similar conclusions can be drawn by examination of the UM2 comparison (Figure 9.10), where the SH distribution falls entirely within the Neanderthal spectrum of variation (no overlap with modern humans except for one specimen) by combining high frequencies of deep anterior fovea and a continuous mid-trigonid crest (Bailey 2002a, b; Bailey et al. 2011 Martinón-Torres et al. 2007a, b, 2012; Zubov 1992a, b). In addition, variability of the SH group is clearly less than that of the Neanderthals. Finally, comparison of LP2 morphology supports the notion that Neanderthals and European Middle Pleistocene populations present a characteristic conformation, with an asymmetrical contour, a mesially displaced metaconid, and accessory lingual cusps in association with a continuous transverse crest (Bailey and Lynch 2005; Genet-Varcin 1962; Martinón-Torres et al. 2006; Patte 1959). However, these traits are polymorphic and not exclusive to this lineage. As it happens with other skeletal parts, some primitive features become "typical Neanderthal" because of their distinct combination and high frequencies of expression (e.g., Bermúdez de Castro et al. 2012; Franciscus and Trinkaus 1995). Thus, the *H. sapiens* spectrum for LP2 covers derived structures exclusive to this species, plus typical morphologies of the Middle Pleistocene populations of Europe and Neanderthals. Again, variability of the SH group would be lower than that of the Neanderthal group.

Summarizing, we can state that with the exception of milder UI1 shoveling and dental tubercles, the SH sample displays typical Neanderthal morphologies, apart from features that make the SH group relatively more derived than some contemporaneous and later groups. In dental classes like UC or UI2, and in accordance with previous findings (Gómez-Robles et al. 2007, 2008; Martinón-Torres et al. 2012), the appearance of the traits in SH specimens are even more pronounced than in the Neanderthal group. In other dental classes, e.g., UM3s, SH populations would fall within the range of variation of modern groups in their strong dental reduction, evinced not only in size decrease of the posterior teeth but in the loss of major cusps (Bermúdez de Castro 1986, 1988; Bermúdez de Castro and Nicolás 1995; Martinón-Torres et al. 2012). Thus, SH dentitions would not fit in a theoretical framework where earlier populations are

less Neanderthal-like than more recent ones, like the accretion process would predict and is observed in other skeletal elements (e.g., Harvati et al. 2010; Hublin 2009). Also in contradiction with this model, the data presented here do not support the notion that Neanderthals show less morphological variability than Middle Pleistocene groups (Hublin 1998; Maureille and Houët 1998; Trinkaus 1983, 1993). With the exception of the UC, intrapopulational variability of SH is similar or less than that of the Neanderthal sample. Hopefully, future discoveries will enrich the hominin fossil record for the European Middle Pleistocene to allow a more precise assessment of variability in these groups. It may be that the SH group is not representative of European Middle Pleistocene hominins, and represents a distinct lineage related to Neanderthals – though also different from them and other Middle Pleistocene groups (Arsuaga 2009; Martinón-Torres et al. 2012; Tattersall 2011). The climatic instability of the Middle Pleistocene and hard glacial conditions of the Upper Pleistocene could have favored a scenario of fragmentation and isolation (Dennell et al. 2010; Hublin and Roebroeks 2009), with eventual speciation in some branches. In this case we would be observing more than one hominin lineage in the Middle Pleistocene and again, the accretion process would not be enough to explain the variability observed in the *H. heidelbergensis* paradigm.

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10 *What does it mean to be dentally "modern"?*

SHARA E. BAILEY AND
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> The decisive factors in each attempt at tracing the line of human evolution are found in paleontological evidence. Nowhere can it be demonstrated as clearly as in the dentition.
>
> *Weidenreich (1937:2)*

10.1 Introduction

Whether or not dental traits could contribute to our understanding of modern human origins was debated in the first half of the last century (e.g., Boule 1923; Boule and Vallois 1957; Keith 1924, 1925; Krogman 1927; Patte 1959; Weidenreich 1937). Because of the highly debated role of Neanderthals (*H. neanderthalensis*) in human ancestry, the focus of modern human origins research has often revolved around contrasting these two species, primarily in skeletal, and especially cranial, features (Churchill and Trinkaus 1990; Frayer 1992; Harvati 2003; Holliday 1999; Howell 1951; Rak et al. 2002; Schwartz and Tattersall 1995; Tattersall and Schwartz 1999; Trinkaus 1986). Until recently, comparative dental studies between Neanderthals and *H. sapiens* focused primarily on the anterior teeth (e.g., Crummett 1995). It was generally assumed that the postcanine teeth of the two groups were similar (Smith 1976). However, in the past decade, additional dental characters have been identified that are relevant to assessing specifically the relationship between Neanderthals and *H. sapiens* and more broadly the question of modern human origins.

Research continues to support the position that Neanderthals possess anterior teeth that are significantly larger than those of *H. sapiens*, both absolutely and relatively (Brace 1967; Bytnar et al. 1994; Trinkaus 1978; Wolpoff 1971). Furthermore, these differences are due specifically to larger buccolingual

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Table 10.1. *Summary of key dental morphological traits that distinguish Neanderthals from H. sapiens*

Tooth	Trait	Neanderthals	*Homo sapiens*
Upper			
I1 and I2	Shoveling, labial convexity, tuberculum dentale	High frequency and expression; frequently co-occur	Low frequency and expression; rarely co-occur
M1	Relative occlusal polygon area	Small (<30% of crown base area)	Large (>30% of crown base area)
	Crown shape	Skewed	Square
Lower			
M1-M3	Trigonid crests	Nearly ubiquitous	Low frequency to absent
M1	Crown outline	Rounded	Angular
Dm2	Crown outline	Rounded	Angular

Source: Reproduced from Bailey et al. (2009).

dimensions. Bytnar et al. (1994) found significant differences in the relative buccolingual dimensions (anterior:posterior) between Neanderthals and early *H. sapiens* in the Near East, even though, according to Rak (pers. comm. 2011), the anterior-posterior length of the dental arcade for Neanderthals and *H. sapiens* do not differ significantly. Tooth size proportions along the molar tooth row also distinguish Neanderthals from *H. sapiens;* in the former the pattern M1<M2>M3 is most common, but in the latter M1>M2>M3 is generally the rule (Trinkaus et al. 2003). Still, tooth size alone is not a foolproof means of identifying Neanderthals versus *H. sapiens* (especially in the context of isolated teeth), since there is so much overlap between the two groups (Henry-Gambier et al. 2004). Frayer (1978) demonstrated that the diminutive size of *H. sapiens* teeth (in Europe) is a recent phenomenon – starting with the Late Upper Paleolithic. It remains to be seen whether differences in metric proportions between Neanderthals and *H. sapiens* appear at the origin of our species or whether they, like overall tooth size, are the result of later evolution.

Dental nonmetric traits (e.g., Bailey 2002a, 2004a; Bailey et al. 2011, 2005; Olejniczak et al. 2008) are more informative than metric traits in differentiating Neanderthals from *H. sapiens* (see Table 10.1 for summary of key traits that distinguish the two groups). Some of these traits are found in earlier hominins (Martinón-Torres et al. 2008; Gómez-Robles et al. 2010), while others appear to be unique to Neanderthals (Bailey 2004b; Bailey and Lynch 2005; Bailey et al. 2011; Gómez-Robles et al. 2007). In some cases (e.g., lower premolar and incisor morphology), it is the combination of features that distinguishes Neanderthals from *H. sapiens* and other fossil hominins, not the presence or

absence of a particular trait (Bailey 2006). In contrast to opinions a few decades ago, it is clear that while dentally similar (at least compared to apes and early hominins), Neanderthals and *H. sapiens* differ enough to be correctly identified by nonmetric dental traits alone (Bailey et al. 2009).

When attempting to identify isolated teeth in the fossil record, Trinkaus (2005) has argued that a discussion of modern human origins should focus not on Neanderthals but on the earliest modern humans. The fossil record for modern humans now spans 200,000 years (Shea et al. 2007), or more if the teeth from Qesem cave (Israel) represent the earliest members of our species (Hershkovitz et al. 2010). Given the chronological depth and number of specimens in the fossil record, we can now evaluate the dental morphology of *H. sapiens* in a spatial and temporal context.

Scott and Turner (1997) summarized the range of many nonmetric dental traits in recent *H. sapiens.* An examination of even a few of the best known traits (e.g., Carabelli's cusp, hypocone reduction) shows that the range in recent humans is wide, and that it would be difficult to characterize *H. sapiens* by any *one* set of crown characters. However, by design, traits in the Arizona State University Dental Anthropology System (ASUDAS: Turner et al. 1991), which is the basis of the Scott and Turner (1997) study, are present and *variable* among geographic groups. Traits that are invariable (i.e., all groups either possess or lack them) are of little value for biological distance studies. As a result, there has been little focus on traits that are shared among all *H. sapiens* (to the exclusion of other fossil hominins) or those that are absent.

The lack of research focus on the dental distinctiveness of *H. sapiens* leads to a number of questions, two of which are the focus here: (1) Are there dental crown characters or a suite of characters that distinguish *Homo sapiens* from earlier or contemporaneous hominins? and (2) If so, when during the course of human evolution does that pattern emerge? To provide a context for interpreting dental variation within our species over time and across geographic regions, we examined dental morphology in extant and fossil *H. sapiens*, as well as non-*sapiens Homo*. We use this information to test the hypothesis that distinctive "modern" characters can be identified in *H. sapiens* and that these characters appear in the earliest *H. sapiens* fossils.

10.2 Materials and methods

Samples in this study include (1) *Homo erectus senu lato* (i.e., African and Asian forms spanning the Early–Middle Pleistocene); (2) *"Homo heidelbergensis" sensu lato* (Middle Pleistocene nonerectine from Europe and Africa pre-dating 300 000 BP) (see Hublin 2009 for discussion); (3) *H. neanderthalensis* (earlier

Table 10.2. *Samples used in this study*

Early *H. sapiens* (65,000–160,000 BP)
Jebel Irhoud, Klasies River Mouth LBS, Sea Harvest, Die Kelders, Equus Cave, Blombos, Mumba*, Eyasi*, Qafzeh, Skhul
Upper Paleolithic (~35,000–12,000 BP)
Oase, Mladeč, Vindija, Fontechevade, La Ferrassie, Derava 'Skala, Istallo, Bacho Kiro, Grotte de Rois, Kostenki, Sunghir 2,3, Qafzeh, Roc de Combe, Lagar Velho, Dolní Věstonice, Pavlov, Abri Pataud, Abri Blanchard, Abri Labatut, Meslingtal, Grotte des Abeilles, L'espugue, La Gravette, Balla Barlang, Bervavolgy, Gruta do Caldeirão, Cisterna, La Madeleine, Peche de la Boissiere, Farincourt, Laugerie Basse, St. Germaine-la-Rivière, Kostenki, Brassempouy*
Recent *H. sapiens*
Sahul-Pacific (Australia, New Guinea), Western Eurasia (Greece, Crete, Hungary, Yugoslavia, Bulgaria, Britain, Austria, Islands, Israel), South Asia, (India, Andaman Islands), North Asia (China, Japan), Sub-Saharan Africa (West Africa, East Africa, Southern Africa)
"H. heidenbergensis" sensu lato
Arago, Mauer, Fontana Ranuccio, Montmaurin, Petralona, Archi, Steinheim, Melpignano, OH22, Cave of Hearths, Thomas Quarries, Hoedjiespunt, Sidi Abderrahmane, Rabat
Early *H. neanderthalensis* (200,000–130,000 BP)
Krapina, Pontnewyyd, Ehringsdorf, Abri Suard
Later *H. neanderthalensis* (70,000–28,000 BP)
Arcy-sur-Cure, Monsempron, Regourdou, St. Cesaire, Gibraltar, Kůlna, Ochoz, Malarnaud, Petit Puymoyen, Pech de l'Aze, Hortus, Taubach, La Fate, Roc de Marsal, Monte Fenera, Grotte Taddeo, Grotte Poggio, Guattari, Saccopastore, Vindija, Spy, Le Moustier, Mongaudier, La Quina, Combe Grenal, Châteauneuf, Marillac, Obi Rakhmat, Subalyuk, La Ferrassie, Amud, Kebara, Shanidar, Tabun

Note:
* Morphological information taken from published literature: Protsch 1981 (Eyasi), Bräuer and Mehlman 1988 (Mumba), Henry-Gambier et al. 2004 (Brassempouy).

and later forms); (4) early *Homo sapiens* from Africa and West Asia; (5) Upper Paleolithic *Homo sapiens* from Europe and Central Asia; and (6) recent *Homo sapiens* representing major geographic populations. Table 10.2 provides the sites (fossils) or regions (recent humans) that compose the samples. Trinkaus (2005) provides a detailed discussion of the context and dating of many of the early *H. sapiens* specimens included here. Not all have been dated directly, but we include them until future studies determine their temporal status.

More than 200 nonmetric dental traits can be scored in humans (Morris 1965). The Arizona State University Dental Anthropology System (ASUDAS) (Turner et al. 1991) has standardized trait expression for 32 crown traits and identified "key" teeth for scoring variation. Traits standardized by the ASUDAS are those that can be easily and reliably scored, endure even in moderately worn teeth, likely have a high genetic component, exhibit little or no sexual

Table 10.3. *Traits used in this study and their sources (see text for explanation)*

Scott and Turner (1997) recent humans	Irish (1993) Sub-Saharan Africa only	Bailey (this study) Recent humans (RH) and/or fossil hominins (FH)
UI1 Shovel shape	UI1 Labial convexity	UI1 Shovel shape (FH)
UM1 Carabelli's cusp	UI1 Double shovel	UI1 Labial convexity (RH,FH)
Three-cusped UM2	UI2 Tuberculum dentale	UI1 Double shovel (RH,FH)
LM1 Cusp 6	UC Mesial ridge	UI2 Tuberculum dentale (RH,FH)
LM1 Cusp 7	UM1 Cusp 5	UC Mesial ridge (RH, FH)
LM1 DW	LM1 Cusp 6	UM1 Carabelli's cusp (FH)
Fissure pattern LM2	Four-cusped LM1	Three-cusped UM2 (FH)
Four-cusped LM1, LM2		UM1 Cusp 5 (RH, FH)
		LP2 Asymmetry (RH, FH)
		LP2 Transverse crest (RH, FH)
		LP2 Lingual cusp number (RH, FH)
		Fissure pattern LM2 (FH)
		LM Middle trigonid crest (RH, FH)

dimorphism, and are variable among recent human groups (Scott and Turner 1997; Turner et al. 1991). We used a combination of ASUDAS traits and those identified as useful in discriminating among Middle–Late Pleistocene hominins (Bailey 2002b). Certain ASUDAS traits were excluded from study because (1) intact dentitions are necessary for scoring (e.g., winging); (2) homology of trait expression is uncertain [e.g., protostylid (Skinner et al. 2009)]; or (3) the trait has very limited distribution among recent and fossil humans [e.g., Uto-Aztecan premolar (Morris et al. 1978)]. For ASUDAS traits, we examined trait frequencies only on the "key" teeth identified in Turner et al. (1991), except for the middle trigonid crest, which has shown important frequency differences on all three lower molars.

Table 10.3 provides a list of traits and their sources. All fossil hominin data were collected by Bailey (2002; this study) from direct observation on casts or original fossils or, in very few cases as noted, from photographs or descriptions of the originals. To make direct comparisons between fossil and recent humans, where applicable, we calculated frequencies based on breakpoints from Scott and Turner (1997). For traits not covered in Scott and Turner, we calculated frequencies based on breakpoints used by Irish (1993). Recent human data were gleaned from three sources: Scott and Turner (1997), Irish (1993), and Bailey (this study).

The data set of Scott and Turner (1997) includes frequencies of nine ASUDAS crown traits in five major geographic regions (Table 10.4): Sino-America

Table 10.4. *Variation (ranges of mean frequencies) of most commonly used nonmetric dental crown characters in recent humans. Mean frequencies for samples are summarized from Scott and Turner (1997)*

	Western Eurasia	Sub-Saharan Africa	Sino-Americas	Sunda-Pacific	Sahul-Pacific	**World Range**
UI1 shovel (3–6)	3.0–53.7	9.6–14.9	22.6–85.8	27.9–37.2	5.4–6.5	**3.0–85.8**
UM1 Carabelli's trait (5+)	4.4–30.1	12.3–20.0	1.9–18.0	15.9–17.2	3.2–18.4	**1.9–30.1**
Three-cusped UM2 (< 2)	13.6–33.7	0.0	8.6–26.5	0–11.8	1.8–25.5	**0–33.7**
LM1 Cusp 6 (1–5)	1.9–11.2	8.6–18.8	11.2–39.6	17.1–52.0	5.4–52.3	**1.9–52.3**
LM1 Cusp 7 (1–4)	1.6–13.6	12.3–42.9	4.5–10.0	5.8–19.2	5.6–8.4	**1.6–42.9**
LM1 DW (3)	5.6–24.8	28.6–50.0	23.6–55.5	30.3–24.7	38.5–41.1	**5.6–55.5**
Y-Pattern LM2 (Y)	1.5–27.8	26.7–68.7	3.5–20.7	10.4–18.3	3.6–9.1	**1.5–68.7**
Four-cusped LM1 (4)	3.4–19.1	0.4–4.0	0.3–9.4	0–1.9	2.4–14.9	**0–19.1**
Four-cusped LM2 (4)	56.2–94.6	16.6–75.1	32.9–64.9	44.4–50.4	44.2–61.4	**16.6–94.6**

(North Asia and the Americas), Western Eurasia (Europe, India, West Asia, and the Caucasus), sub-Saharan Africa (Western and Southern Africa), Sahul-Pacific (Australia, New Guinea, and Tasmania), and Sunda-Pacific (Southeast Asia, Polynesia, and Micronesia). Eleven additional traits are derived from Bailey's data set (this study), made up of smaller samples (n = 10–50) from the same regions in Scott and Turner (1997), sans the Americas (Table 10.5); they include ASUDAS traits not covered in Scott and Turner (1997) and three others that are not part of the ASUDAS (P_4 asymmetry, P_4 transverse crest, P_4 fissure pattern). Because the sub-Saharan Africa data sets of Scott and Turner (1997) and Bailey are small, we replaced them with Irish's (1993) larger sample of sub-Saharan Africans (up to 500 individuals) where presence/absence breakpoints were in agreement (indicated in tables). We assume interobserver error does not significantly affect the results for two reasons: (1) Bailey and Irish were both trained by Turner; and (2) a comparison of trait frequencies collected on the same data sets between Bailey and Irish [e.g., the Krapina dental material (Irish 1998)] indicates there is little difference between the two authors, at least at the presence/absence level used in this study.

Table 10.5. *Frequencies of ASUDAS and non-ASUDAS traits for recent humans [not presented in Scott and Turner (1997)]. Where noted (*) average and ranges for Sub-Saharan Africa data are from Irish (1993). Otherwise all data are from Bailey (this study)*

	Western Eurasia	South Asia	Sub-Saharan Africa	North Asia	Sahul-Pacific	**World Range**
UI1 labial convexity (2–4)	7.8	41.7	55.8 (0–75)*	12.5	0.0	**0–75**
UI1 double shovel (2–6)	19.6	4.2	1.3 (0–8.3)*	62.5	12.5	**0–62.5**
UI2 tuberculum dentale (2–6)	27.9	50.0	35.9 (0–100)*	0.0	20.0	**0–100**
UC' mesial ridge (1–3)	2.6	0.0	17.0 (0–40.6)*	0.0	0.0	**0–40.6**
UC' DAR	32.1	20.0	49.2 (20.3–70)*	42.9	75.0	**20–70**
UM1 Cusp 5 (2–5)	30.3	44.7	23.1 (0–40.0)*	42.9	88.2	**0–88.2**
LP2 asymmetry (>1)	0.0	0.0	0.0	0.0	0.0	**0**
LP2 transverse crest	1.5	6.5	0.0	10.0	5.6	**0–10**
LP2 lingual cusp number (>1)	55.2	37.5	69.1 (40–86.2)*	50.0	87.5	**37.5–87.5**
LP2 fissure pattern (U)	42.9	51.9	23.3	40.0	75.0	**23.3–75**
LM1 midtrigonid crest (2)	2.0	0.0	5.0	0.0	0.0	**0–5.0**
LM2 midtrigonid crest (2)	0.0	0.0	0.0	0.0	0.0	**0**
LM3 midtrigonid crest (2)	0.0	0.0	0.0	0.0	0.0	**0**

Note: Composition of Bailey's samples: Western Eurasia: Europe, Israel and North Africa; South Asia: India, Andaman Islands; Sub-Saharan Africa: Southern Africa; North Asia: China, Japan; Sahul-Pacific: Australia, New Guinea.

10.3 Results

10.3.1 Dental morphology

10.3.1.1 Labial convexity UI1

Worldwide variation in labial convexity is not reported in Scott and Turner (1997). In recent humans from Bailey's sample, the frequency of UI1 labial convexity ranges from 0 percent to 41.7 percent. The lowest frequencies are for North Asia and Sahul-Pacific, while the highest are observed in South Asia (India). Irish (1993) reports higher frequencies (up to 75 percent) for UI1 labial convexity in sub-Saharan Africa, but this could be due to differences in scoring the trait at the presence/absence dichotomy.

Fossil hominins exhibit a wide range of trait presence (11.8–100 percent). The early *H. sapiens* sample is at the high end of the recent human range (44.4 percent), whereas the frequency drops substantially (to the level observed in North Asian) by the time of Upper Paleolithic *H. sapiens* (11.8 percent). This provides a notable contrast to the high frequencies in *Homo erectus* (60 percent) and Neanderthals (100 percent).

Table 10.6. *Nonmetric trait frequencies (ASUDAS and non-ASUDAS traits) in later fossil Homo*

	H. erectus	*H. heidelbergensis*	Early *H. sapiens*	Upper Paleolithic *H. sapiens*	Early *H. neanderthalensis*	Later *H. neanderthalensis*	**Fossil sample range**
UI1 shovel (3–6)	40.0 (7)	*	14.3 (7)	0.0 (13)	100 (14)	81.8 (11)	**0.0–100**
UI1 labial convexity (2–4)	66.7 (6)	*	44.4 (9)	11.8 (17)	100 (14)	91.7 (12)	**11.8–100**
UI1 double shovel (2–6)	0.0 (6)	*	0.0 (8)	0.0 (17)	0.0 (14)	0.0 (9)	**0.0**
II2 tuberculum dentale (2–6)	0.0 (2)	100 (2)	60.0 (5)	33.3 (9)	100 (13)	90.9 (11)	**0.0–100**
UC distal accessory ridge (2–5)	66.7 (3)	100 (1)	100 (2)	100 (6)	28.6 (7)	62.5 (8)	**28.6–100**
UC mesial ridge (1–3)	0.0 (4)	0 (1)	0.0 (5)	12.5 (8)	33.3 (12)	37.5 (8)	**0.0–37.5**
UM1 Carabelli's (5+)	0.0 (1)	40.0 (2)	25.0 (8)	31.8 (22)	54.5 (11)	28.6 (14)	**0–54.5**
Cusp 5 UM1 (1–5)	0.0 (2)	40.0 (2)	42.9 (7)	57.9 (19)	70.0 (10)	53.8 (13)	**0.0–70**
3-Cusped UM2 (< 2)	0.0 (8)	0.0 (11)	0.0 (12)	0.0 (21)	0.0 (13)	0.0 (20)	**0**
LP2 Asymmetry (>1)	21.4 (14)	33.3 (9)	40.0 (6)	0.0 (8)	92.9 (14)	63.2 (12)	**0.0–92.9**
LP2 Transverse crest	23.1 (13)	50 (10)	16.7 (6)	21.4 (14)	92.3 (13)	63.2 (19)	**16.7–92.3**
LP2 lingual cusp number (>1)	88.9 (9)	71.4 (7)	66.7 (6)	38.5 (13)	92.9 (14)	91.7 (12)	**38.5–92.9**
LP2 Fissure Pattern (U)	0.0 (6)	0.0 (4)	40.0 (5)	25.0 (12)	0.0 (14)	0.0 (12)	**0–40.0**
LM1 middle trigonid crest (>1)	0.0 (12)	66.7 (9)	20.0% (10)	0.0 (27)	100 (18)	94.7 (17)	**0.0–100**
LM2 middle trigonid crest (>1)	0.0 (11)	60.0 (10)	0.0 (7)	0.0 (26)	92.9 (14)	85.7 (14)	**0.0–92.9**
LM3 middle trigonid crest (>1)	0.0 (3)	40.0 (5)	0.0 (5)	0.0 (16)	83.3 (6)	80.0 (11)	**0.0–83.3**
LM1 Cusp 6 (1–5)	28.6 (7)	25.0 (4)	0.0 (11)	20.0 (25)	40.0 (10)	37.5 (16)	**0.0–40.0**
LM1 Cusp 7 (1–4)	50 (12)	0.0 (7)	50.0 (16)	6.1 (33)	41.2 (17)	16.7 (24)	**0–50.0**
LM1 DW (3)	57.0 (7)	0.0 (5)	42.9 (7)	4.5 (22)	0.0 (13)	5.6 (18)	**0–57.0**
LM2 Y-pattern	92.3 (13)	63.6 (11)	85.7 (7)	42.9 (28)	66.7 (15)	81.0 (21)	**42.9–92.3**
Four-cusped LM2 (4)	0.0 (13)	0.0 (13)	0.0 (16)	5.3 (38)	0.0(17)	0.0 (36)	**0–5.3**
Four-cusped LM2 (4)	0.0 (13)	0.0 (14)	9.1 (11)	40.9 (22)	0.0 (15)	0.0 (26)	**0–49**

Note: Number of individuals in parentheses.

10.3.1.2 Shoveling UI1

Scott and Turner (1997) report a range of shovel-shaped incisors in recent humans from 3 percent to 85.8 percent. Their frequencies are based on a breakpoint of grade 3 and above – which does not include "trace" or "slight." The highest frequencies are found in North Asia and the Americas; the lowest are in Western Eurasia and Sahul-Pacific. Irish (1993) uses a less conservative breakpoint for presence (presence = grades 2–7) so his data are not included here.

Fossil hominins exhibit a wide range of variation in shoveling (0–100 percent). The earliest *H. sapiens* exhibit low frequencies of UI1 shoveling (14.3 percent), while it is absent in the Upper Paleolithic *H. sapiens* group. This is in stark contrast to the much higher frequencies in *Homo erectus* (50 percent) and Neanderthals. All early Neanderthals and 81.8 percent of later members of the species express the shoveling variant.

10.3.1.3 Double shoveling UI1

Scott and Turner (1997) note that the worldwide range for double shoveling is 0 percent to 70 percent, with the lowest frequencies (0–15 percent) in Western Eurasian, sub-Saharan African, Sunda-Pacific, and Sahul-Pacific groups. Intermediate frequencies (20–40 percent) characterize East and North Asia and the American Arctic. By far the highest frequencies are found among Native Americans (55–70 percent). Bailey (this study) found the highest frequency in North Asia (62.5 percent) and the lowest (0 percent) in Southern Africa. Irish (1993) also found very low frequencies of double shoveling in sub-Saharan Africans, where the group average was 1.3 percent, with a range from 0 percent to 8.3 percent. Double shoveling is absent from all of our fossil hominin groups.

10.3.1.4 Tuberculum dentale UI2

Scott and Turner (1997) do not provide a worldwide range for the UI2 tuberculum dentale trait. In Bailey's recent human data set, the range is 0 to 50 percent. North Asia shows the lowest frequency and South Asia (India) the highest. Sub-Saharan African groups have an average of 35.9 percent, and a large range in trait frequencies (0 percent to 100 percent; Irish 1993).

Early *H. sapiens* and Upper Paleolithic *H. sapiens* have frequencies that are on the high end or slightly higher than Bailey's recent human range (60.0 percent and 33.3 percent, respectively). By contrast, UI2 tuberculum dentale is absent in *Homo erectus*. Both groups differ markedly from Neanderthals, who almost invariably express this trait on the anterior teeth (90.9–100 percent).

10.3.1.5 Canine mesial ridge

Scott and Turner (1997) do not provide a worldwide range for the canine mesial ridge [a.k.a. Bushman canine (Morris 1975)]. None of Bailey's non-African recent samples shows trait presence, while the average frequency for sub-Saharan African samples is 17 percent (range 0%–40.6%; Irish 1993). Not surprisingly, the trait lives up to its original name with the highest frequencies in the San and Khoikhoi.

The canine mesial ridge is absent from the early *H. sapiens* sample but occurs in a frequency close to the sub-Saharan African average in the Upper Paleolithic sample (12.5 percent). Early and later Neanderthals, on the other hand, show frequencies at the high end of the sub-Saharan range (33.3 percent and 37.5 percent, respectively). The trait was not observed on any of four *Homo erectus* upper canines.

10.3.1.6 Canine distal accessory ridge

Scott and Turner (1997) do not report a range in worldwide frequencies for the canine distal accessory ridge. Bailey's recent human data set shows a range of 20–75 percent, with the highest frequencies in Sahul-Pacific groups and the lowest in South Asians.

In fossil hominins, the frequency of the canine distal accessory ridge ranges from 28.6 percent to 100 percent. In both early and Upper Paleolithic *H. sapiens,* the trait appears to be ubiquitous and most similar to the recent Sahul-Pacific sample. It is much lower in *Homo erectus* and lowest in Neanderthals.

10.3.1.7 Carabelli's trait UM1

Scott and Turner (1997) report worldwide frequency data for the cusp form of Carabelli's trait (grades 5–7); other studies commonly use a breakpoint of 0–1/2–7. The cusp form ranges from 1.9 percent to 30.1 percent in Scott and Turner's (1997) worldwide sample. The lowest frequency occurs in Sino-Americans while the highest frequency is for Western Eurasians.

Using the same breakpoint for fossil hominins, the range of cusp forms is between 0.0 percent and 54.5 percent. Early *H. sapiens*, Upper Paleolithic *H. sapiens*, and later Neanderthals fall in the middle of the fossil hominin range (25 percent, 31.8 percent, and 28.6 percent, respectively), and at the high end of the recent human range. Carabelli's cusp is present in an even higher frequency in early Neanderthals (54.5 percent), while it is absent from the single *H. erectus* UM1 that could be scored.

10.3.1.8 Cusp 5 UM1

According to Scott and Turner (1997), the worldwide range of variation for UM1 cusp 5 is 10–60 percent. Western Eurasian and Sino-American groups

have frequencies between 10 and 25 percent while the trait is more common in Sunda-Pacific (30–40 percent) and Sahul-Pacific (40–60 percent) groups. These numbers are generally in line with Bailey's recent human data that suggest a range of 20.6–88.2 percent, with the lowest frequency in Western Eurasia and the highest in Austral-Asia. Sub-Saharan Africans fall in the low to middle portion of this range (average: 23.1 percent, range: 0–40 percent; Irish 1993), which is similar to that found by Bailey (28.6 percent) for Southern Africans.

In fossil hominins, UM1 Cusp 5 ranges from 0.0 percent to 70 percent. Early *H. sapiens* and Upper Paleolithic *H. sapiens* show frequencies in the middle of the recent and fossil human ranges (42.9 percent and 57.9 percent, respectively). Neanderthals, on the other hand, are at the high end of the recent human range and possess the highest frequencies of all fossil hominins (70 percent). The two *Homo erectus* that could be scored lack the trait.

10.3.1.9 Three-cusped upper molars UM2

The complete or near-complete loss of the hypocone, resulting in three-cusped upper second molars, occurs in relatively low frequencies in all recent groups (0–33.7 percent). Scott and Turner (1997) report the lowest frequency in sub-Saharan Africans and the highest in Western Eurasians (up to 33.7 percent). Bailey's data also show the lowest frequency in Africa, while Irish's (1993) data use a less conservative breakpoint (grades 0–2 counted as absence), which does not allow direct comparison with Scott and Turner (1997).

None of the UM2s in our fossil hominin sample exhibited complete loss of the hypocone (grade 0–1). However, four Upper Paleolithic *H. sapiens* individuals (18.2 percent) show an incipient form, with a hypocone reduced to the point of a small cuspule (grade 2).

10.3.1.10 Lingual cusp number LP2

Scott and Turner (1997) do not report worldwide frequencies for multiple lingual LP2. Bailey's data show a range from 37.5 percent to 87.5 percent. Irish's (1993) data show nearly as much variation in sub-Saharan Africans alone (40–86.2 percent). Western Europeans and South Asians exhibit the lowest frequencies, while the Sahul-Pacific groups have the highest.

A range similar to that of modern humans can be found in fossil hominins (38.5–92.9 percent). The Upper Paleolithic sample shows the lowest frequency (38.5 percent), which is similar to that in South Asia and Western Europe. Early *H. sapiens* samples have an intermediate frequency (66.7 percent), but one that is still lower than that of *Homo erectus* and *H. neanderthalensis*.

10.3.1.11 Premolar shape LP2

Lower premolar shape is not included in the ASUDAS (Turner et al. 1991). However, Bailey (2002a) found this trait discriminates between Neanderthals and *H. sapiens* so it is included here. All recent *H. sapiens* exhibit rounded and generally symmetrical LP2s. Marked (>grade 1) asymmetry is absent in the recent *H. sapiens* sample.

In our fossil hominin sample, the frequency of marked asymmetry ranges from 0.0 percent to 92.9 percent. Both early and Upper Paleolithic *H. sapiens* lack marked asymmetry, while in *Homo erectus* it is present in relatively low frequency (18.2 percent). Only early and later Neanderthals show a high frequency of this particular premolar shape (63.2–92.9 percent, respectively).

10.3.1.12 Transverse crest LP2

The expression of a crest that connects the buccal and lingual cusps of the LP2 has not been standardized by the ASUDAS. Therefore, the worldwide distribution is based solely on Bailey's data. We found this trait to be rare in recent humans. Only one individual in each of three groups (North Asia, South Asia, and Sahul-Pacific) exhibited a continuous crest, leading to frequencies of 10 percent, 6.5 percent, and 5.6 percent, respectively.

In fossil hominins, the range is 16.7 percent to 92.3 percent. The lowest frequency is in early *H. sapiens,* followed by Upper Paleolithic *H. sapiens* and *Homo erectus* (20 percent and 21.4 percent, respectively). *H. heidelbergensis* and later Neanderthals have much higher frequencies (50 percent and 63.2 percent, respectively) while early Neanderthals have the highest.

10.3.1.13 Fissure pattern LP2

The form of the fissure dividing the buccal and lingual cusps is not completely independent of the transverse crest (if a crest is present the fissure is obscured), but, when the transverse crest is absent, the fissure takes a variety of forms, including H, Z, U, Y, or X (Figure 10.1). The U-shaped pattern reflects the absence of a transverse crest and, to some extent, talonid reduction. Thus, it is often associated with a simplified occlusal morphology. The fissure pattern of the P_4 has not been standardized by the ASUDAS and data are not provided in Scott and Turner (1997) or in Irish (1993).

Bailey's data set shows a range of 23.3 percent to 75 percent for presence of the U-shaped fissure. It was lowest in sub-Saharan Africans and highest in Sahul-Pacific populations. The high frequency in Sahul-Pacific groups may be surprising since they have rather complex lower premolars. In this case, the teeth have multiple lingual cusps combined with a reduced talonid, which results in the U-pattern (Figure 10.1).

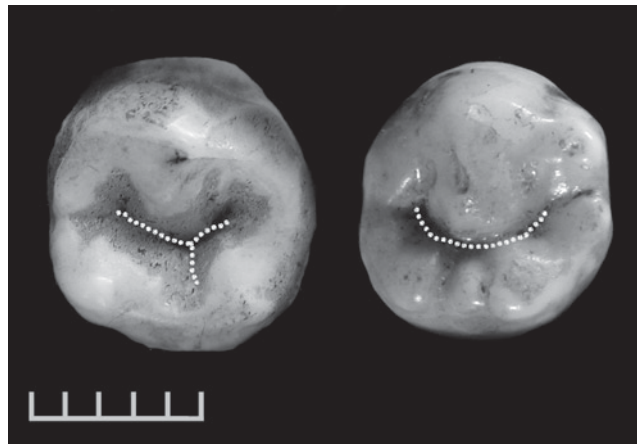

Figure 10.1. Lower fourth premolars showing variation in fissure pattern: Y-pattern on the left and U-pattern on the right (Europe and Australia, respectively).

In the fossil hominin sample, the U-shaped fissure pattern is present only in *H. sapiens* groups. The predominant fissure pattern in the fossil hominin groups was an H.

10.3.1.14 Middle trigonid crest LM1–3

The middle trigonid crest was added to the ASUDAS in 1993 (Wu and Turner 1993), but worldwide trait frequencies are not reported in Scott and Turner (1997). Bailey's data set shows a low frequency of the continuous crest form in recent LM1 (0.0–5 percent) and trait absence in LM2–LM3. Bailey's Southern African sample shows the highest frequency. Irish (1993) reports somewhat higher frequencies in his sub-Saharan Africa sample (up to 11.1 percent, but only LM1 is reported).

The range of variation for the middle trigonid crest in fossil hominins is 0–100 percent for LM1, 0–92.9 percent for LM2 and 0.0–83.3 percent for LM3. Early *H. sapiens* are similar to *Homo erectus* in the frequency of the crest (20 percent), but the trait is absent in the Upper Paleolithic *H. sapiens* sample. The trait is absent from the remaining lower molars of fossil *H. sapiens* as well as *Homo erectus*. Neanderthals are unique among both fossil and recent hominins for their exceptionally high trait frequencies on LM1, LM2, and LM3 (100 percent, 92.9 percent, and 83.3 percent).

10.3.1.15 Cusp 6 LM1

According to Scott and Turner (1997), the worldwide frequencies for LM1 Cusp 6 range between 1.9 percent and 52.3 percent. The lowest frequencies

are found in Western Eurasians while the highest are found in Sunda- and Sahul-Pacific groups. These percentages are similar to the range in Bailey's data set (7–46 percent), with similar low and high frequency groups. The average frequency for sub-Saharan Africa is 9.1 percent (range 0–30 percent; Irish 1993).

In fossil hominins, the range of trait presence is similar to that of recent humans (0.0–40 percent). We did not find Cusp 6 LM1 in any of the early *H. sapiens* individuals, but it occurs in 20 percent of the Upper Paleolithic *H. sapiens* sample. Early and later Neanderthals show similar frequencies for Cusp 6 (40 and 37.5 percent, respectively). While it is lower in the *H. heidelbergensis* sample (25 percent).

10.3.1.16 Cusp 7 LM1

Scott and Turner (1997) report the range of variation in world populations for Cusp 7 LM1 is similar to that of Cusp 6, but the distribution of high and low frequency groups is different. The highest frequencies are found in sub-Saharan Africans (12.3–42.9 percent) while low frequencies characterize the rest of the world (1.6–19.2 percent). Bailey's data set shows similar frequencies and world distribution.

Fossil hominins have a slightly wider range of trait presence for Cusp 7 (0–50 percent). Early *H. sapiens* shares the highest frequency of cusp 7 with *Homo erectus*, but the value drops dramatically in later Upper Paleolithic *H. sapiens*. Early Neanderthals are close (41.2 percent) to early *H. sapiens* and *Homo erectus,* but the frequency drops dramatically in later Neanderthals (16.7 percent). Cusp 7 is absent in the *H. heidelbergensis* sample.

10.3.1.17 Deflecting wrinkle LM1

Scott and Turner (1997) report a range of 5.6 percent to 55.5 percent for the deflecting wrinkle in recent human groups. They found the highest frequencies in Sino-Americans and the lowest in Western Eurasians. Bailey's data show lower overall frequencies and a narrower range of variation (0–22 percent), with the highest frequency in Southern Africans. This pattern probably indicates interobserver error so the best comparisons would be between Bailey's recent and fossil data to assure comparable scoring.

The early *H. sapiens* sample shows a high frequency for the deflecting wrinkle (42.9 percent), outside Bailey's recent human range. The frequency drops to the low end of the recent human range in Upper Paleolithic *H. sapiens* (4.5 percent). *Homo erectus* has a uniquely high (80 percent) frequency of the deflecting wrinkle, whereas it is absent or rare in Neanderthal and *H. heidelbergensis* samples (0–5.6 percent).

10.3.1.18 Y-pattern LM2

The Dryopithecus, or Y-5 pattern, is the ancestral condition for apes and humans. "It is characterized by a five-cusped molar in which cusps 2 (metaconid) and 3 (hypoconid) in contact, creating a Y-shaped fissure pattern." It is retained in high frequencies on LM1 but is less common and more variable on LM2 and LM3 in recent groups. Since the Y-pattern (cusps 2 and 3 in contact) may be present even in four cusped molars, it is referred to simply as the Y-pattern here. Scott and Turner (1997) note the range for the Y-pattern on LM2 in recent humans is rather broad at 1.5–68.7 percent, although most groups fall between 20 and 40 percent. Sub-Saharan Africans have the highest frequencies of LM2 Y-pattern, especially the San (70 percent), while Sino-Americans have the lowest frequencies (10–20 percent). Bailey's data set shows a similar range and distribution of high and low frequency groups. The average for sub-Saharan Africans is 51.7 percent (range 10–59.3 percent; Irish 1993).

In fossil hominins, the Y-pattern on LM2 is retained in much higher frequencies compared to recent human groups. Retention of the Y-5 pattern is highest in *H. erectus* (100 percent). Early *H. sapiens* also have a very high frequency of the Y pattern on LM2 (85.7 percent), while that of Upper Paleolithic *H. sapiens* is about half as high (42.9 percent), but still at the high end of the range for recent humans. Neanderthals (66.7–81 percent) and *H. heidelbergensis* have frequencies that are much higher than in most recent human populations.

10.3.1.19 Four-cusped LM1 and LM2

The loss of the hypoconulid on the lower molars produces a four-cusped molar. Scott and Turner (1997) report worldwide data for four-cusped LM1 and LM2. Most recent human groups maintain high frequencies of five cusps on the LM1; the range for hypoconulid loss on this tooth is 0.0 percent to 19.1 percent. African and Sino-American groups have very low frequencies of four-cusped LM1 (0–3 percent). Western Eurasians have by far the highest frequencies for this trait, which range from 10 to 20 percent. Remarkably, New Guinea populations show the next highest frequency of hypoconulid loss. In fact, Sahul-Pacific groups are second to Western Eurasians in the frequency of four-cusped lower molars.

The frequency of four-cusped molars is considerably higher on LM2, with some recent groups nearing 100 percent. Western Eurasians have the highest frequencies of hypoconulid loss (up to 94.6 percent), while sub-Saharan Africans show the lowest (as low as 16.6 percent). Irish's (1993) data set suggests an even lower frequency in sub-Saharan Africans (11.1–57.1 percent).

Of the fossil hominins in our sample, only one – an Upper Paleolithic *H. sapiens* individual – possesses a four-cusped M_1. The frequency of four-cusped LM2 was higher, but still limited to *H. sapiens*. We observed it in one individual from the early *H. sapiens* sample (9.1 percent) and in nine individuals from

Upper Paleolithic *H. sapiens* (40.9 percent). The loss of the hypoconulid on the lower molars is one of the most significant trends in the evolution of Western Eurasian dental morphology.

10.4 Discussion

10.4.1 The "modern" human dental morphological pattern

One of the biggest challenges in defining what it means to be morphologically "modern" is accommodating the range of variation observed in recent humans. A definition of "modern" based on cranial morphology has proven to be difficult (Wolpoff 1986, 1990). It is also a problem we encountered in characterizing the dental morphology of fossil hominins. Researchers have found so much dental variation within *H. sapiens* that geographic dental patterns have been defined for different geographic groups [e.g., Caucasoid (Mayhall et al. 1982), Mongoloid (Hanihara 1969), sub-Saharan African (Irish 1997) [now Afridont (Irish, this volume)], Indodont (Hawkey 1998), and Eurodont (Scott et al., this volume) and even subdivisions of the "Mongoloid" group: Sinodont/Sundadont (Turner 1983)]. On one end of the spectrum, sub-Saharan Africans retain a primitive dental morphological pattern (Irish 1998; Irish and Guatelli-Steinberg 2003). On the other end of the spectrum, populations from Northeast Asia and the Americas (collectively known as Sinodonts – Turner 1990) are dentally derived relative to other recent groups (Irish 1998; Turner 1990).

Our results demonstrate that none of the dental traits examined is shared by all *H. sapiens* individuals or even populations. Therefore, it is impossible to list a set of traits that define the "modern" human dentition. That recent/living humans exhibit a wide range of dental morphological variation is supported by recent studies of enamel thickness, which is also highly variable in the genus *Homo* (Smith et al. in review). As in dental crown morphology, *H. sapiens* shows so much variation in enamel thickness globally and temporally, it would be impossible to state what it means to be "modern."

On the other hand, we have identified some traits that are present *only* in *H. sapiens*; we have also found some that are absent from all *H. sapiens* groups but are present and variable in non-*sapiens*. From a taxonomic or classificatory perspective these distinctions are important. A discussion of these traits is presented in the following.

10.4.1.1 Upper incisors

While variable across geographic groups, flat featureless upper incisors are found only in samples of *H. sapiens*. In contrast, all non-*sapiens* hominins

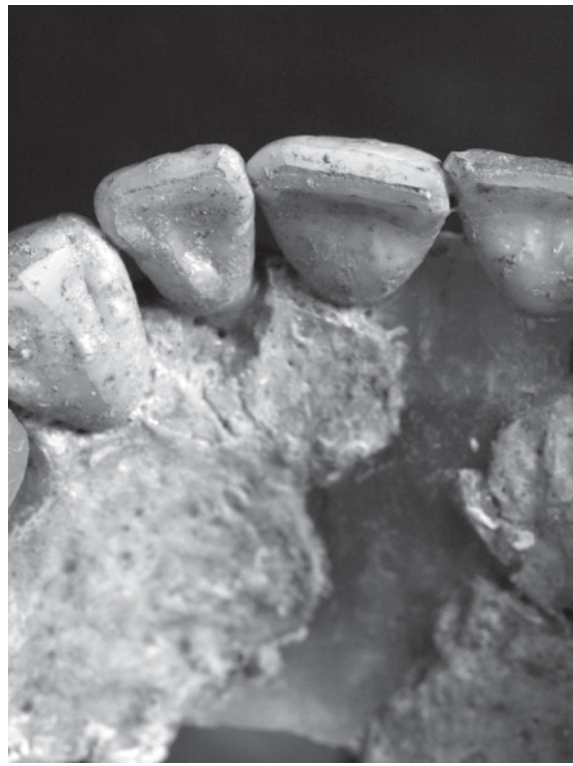

Figure 10.2. "Modern" incisor morphology in early *H. sapiens* (Qafzeh 11). Both UI1 and UI2 are relatively flat and featureless.

exhibit some degree of UI1 shoveling. Labial curvature exceeding grade 1 is nearly ubiquitous in non-*sapiens* fossils, but this has largely been replaced by the flat surfaces of recent sapiens. Tuberculum dentale occurs in relatively high frequencies in both fossil hominins and recent humans but tends to be more pronounced in the former. The co-occurrence of these three traits on a single tooth is a diagnostic character of Neanderthals (Bailey 2006; Mizoguchi 1985) and earlier members of their lineage (Martinón-Torres et al. 2012). An incisor lacking all three traits is diagnostic of *H. sapiens*. This "modern" morphology makes its first appearance in early *H. sapiens* (Figure 10.2) and reaches frequencies similar to that in recent Europeans by the Upper Paleolithic.

Double shoveling was found only in the *H. sapiens* samples. However, the trait is rare or absent outside North Asia and is not present in the earliest members of our lineage. While we found no evidence of double shoveling in early and Upper Paleolithic *H. sapiens*, Liu et al. (2010) described Late Pleistocene incisors from China that exhibit the trait. If the age (34–44 kya

based on electron spin resonance [ESR]) of these specimens is accurate, it would suggest an Upper Paleolithic origin for this trait, which is slightly older than previously suggested (Turner et al. 2000).

10.4.1.2 Canines

With regard to the distal accessory ridge and mesial ridge, there is nothing remarkable about the canine morphology of *H. sapiens* relative to non-*sapiens* hominins. However, in general, fossil hominin canines mirror the morphology of incisors with moderately developed shovel shaping and lingual tubercles, but these traits were not examined here (Bailey 2006). This combination of features can be found in early *H. sapiens* and Upper Paleolithic *H. sapiens,* as well as some recent groups. Yet the opposite condition, that is, a lack of shoveling, lingual tubercles, and distal accessory ridge (basically a flat, featureless canine), is not observed in non-*sapiens* and only appears in some recent human groups.

10.4.1.3 Upper molars

In most respects, the morphology of UM1 in recent *H. sapiens* is similar to that of its fossil predecessors. The frequencies of Carabelli's trait, Cusp 5, and hypocone do not distinguish *H. sapiens* from earlier hominins. Previous studies have shown that *H. sapiens* UM1s are roughly square-shaped with widely spaced cusps (Bailey 2004b; Gómez-Robles et al. 2007); moreover, they possess a metacone that is smaller than the protocone (Quam et al. 2009). These features are also characteristic of later *Homo*, with the exception of Neanderthals, which possess a skewed UM1 shape and narrow intercusp distances. While there are several UM1 features that identify Neanderthals, there is nothing particular about the UM1 crown morphology of *H. sapiens* that would distinguish it from non-Neanderthal later *Homo*.

In many ways the UM2 of *H. sapiens* is similar to that of fossil hominins. We found meaningful differences in only one trait: upper molar cusp number/loss of the hypocone. In our sample, a three-cusped upper molar was observed only on the UM2 and only in recent *H. sapiens* groups. Nearly every recent group expressed this trait; in fact, it reached 30 percent or more in some populations (e.g., Indo-Europeans). In contrast, a three-cusped UM2 was absent in all fossil samples, including early and Upper Paleolithic *H. sapiens*. However, 18.2 percent of the Upper Paleolithic *H. sapiens* sample possessed an incipient form – a greatly reduced hypocone (grade 2) (Figure 10.3). It is tempting to conclude that the complete, or near-complete, loss of the hypocone is a recent phenomenon occurring only in *H. sapiens* since the Upper Paleolithic or later, depending on the presence/absence breakpoint. However, Martinón-Torres et al. (2012) have reported that 33.3 percent of the Sima de los Huesos sample

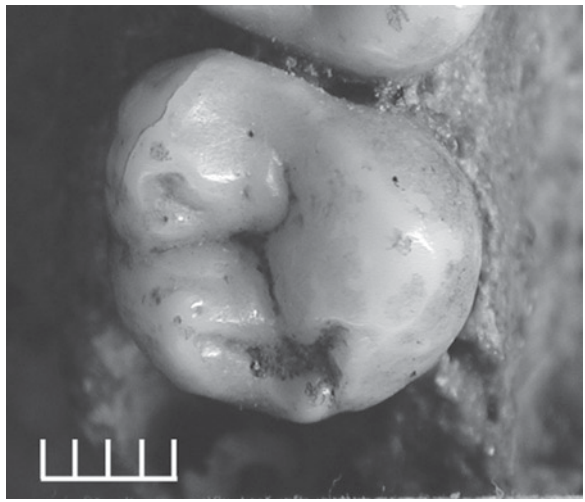

Figure 10.3. A UM2 exhibiting a greatly reduced hypocone (Mlade č1).

exhibit hypocone loss (grade 0–1) and an additional 44 percent exhibit the much reduced form (grade 2) seen in our Upper Paleolithic sample. Therefore, this trait is not diagnostic of our species.

10.4.1.4 Lower premolars

We did not assess variation in LP1 in this study. However, (Gómez-Robles et al. (2008:634) found that *H. sapiens* possesses derived morphology, which includes "a symmetrical and circular premolar outline with a weak or absent talonid" and an "occlusal polygon [that] is large and centrally located due to the buccally-displaced protoconid tip."

We observed similar changes relating to crown simplification in the lower second premolar. In *H. sapiens,* LP2 crowns tend to be symmetrical and circular. They also exhibit weak or absent talonids. The lingual cusp (metaconid) is typically centrally placed, and many of these teeth lack additional lingual cusps. LP2s with a single lingual cusp are found only in *H. sapiens* samples. Two-thirds of the early *H. sapiens* sample possess an LP2 with a single lingual cusp. In contrast, all the lower second premolars in our non-*sapiens* samples possess distal and/or distolingual cusps in addition to the main lingual cusp (metaconid). Martinón-Torres et al. (2012) report that 100 percent of LP2 from Sima de los Huesos possess multiple lingual cusps.

The loss of crown complexity – in particular the simplification of the lingual moiety described previously – has occurred alongside a simplification of

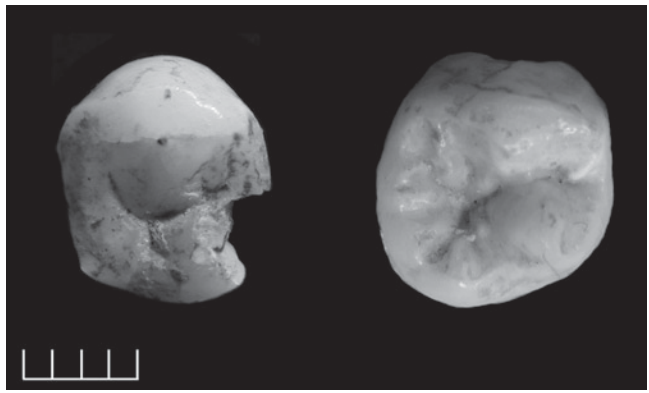

Figure 10.4. "Modern" premolar morphology in early *H. sapiens* (Klasies River Mouth AP6227). The LP2 exhibits a rounded, symmetrical crown, with a U-shaped fissure pattern.

the fissure pattern in *H. sapiens*. The most common H, Y, X, or Z pattern of non-*sapiens* teeth contrasts the more derived, U-shaped fissure observed only in *H. sapiens* (Figure 10.4). We found the earliest example of this simplified pattern in early *H. sapiens* (Klasies River Mouth). The U-shape becomes more common in later *H. sapiens*, especially in groups that have undergone the most dental reduction (Indo-Europeans).

Bailey (2002a) suggested the combination of multiple lingual cusps, a transverse crest, and moderate to marked crown asymmetry is diagnostic and, perhaps, uniquely derived in Neanderthals. The crown outline of *H. sapiens* LP2 seems to have evolved in a different direction to become more circular (rather than asymmetrical or squared), with a single lingual cusp placed centrally rather than mesially – and with a reduced talonid (Bailey 2002a; Martinón-Torres et al. 2006). This combination, together with the U-shaped fissure, may be considered derived for *H. sapiens*. All features appear early in *H. sapiens* evolution, although some (crown symmetry) do not become fixed in these populations until the Upper Paleolithic.

10.4.1.5 Lower molars

Variation in most traits on the lower molars, such as cusp 6 and cusp 7, is variable across recent and fossil hominin groups. Neither the presence nor the absence of these cusps, along with the deflecting wrinkle or form of the LM2 fissure pattern, distinguishes *H. sapiens* from non-*sapiens* groups. Just one trait, loss of a hypoconulid on the LM1 and LM2, is unique to our *H. sapiens* sample. Hypoconulid reduction in the LM2 preceded reduction in the LM1;

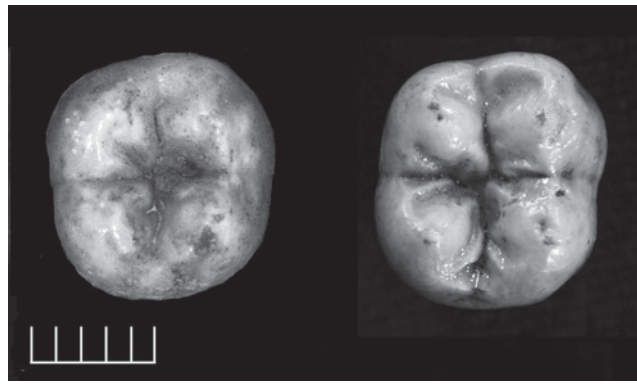

Figure 10.5. "Modern" lower molar cusp morphology (loss of hypoconulid) in early *H. sapiens* (Qafzeh 11: LM2) and Upper Paleolithic *H. sapiens* (La Madeleine: LM1).

a four-cusped LM2 appeared in some of the earliest *H. sapiens* (though see Martinón-Torres et al. 2012), although a four-cusped LM1 was absent until the Upper Paleolithic (Figure 10.5). By the time of the Upper Paleolithic, the frequency of four-cusped LM2 reached 40.9 percent, a value comparable to that in most recent human populations except Western Eurasians, who have a frequency twice that value (>80 percent).

We believe that four-cusped LM1 and LM2 are diagnostically *H. sapiens,* and that the four-cusped LM2 originates at the beginning of our species. However, recently Martinón-Torres and colleagues (2012) report low to moderate frequencies for four-cusped LM1 (9.5 percent) and LM2 (28.6 percent) at Sima de los Huesos. If these data are correct, four-cusped lower molars would be characteristic of *H. sapiens* but not necessarily diagnostic.

The form of the middle trigonid crest may be the only diagnostic feature of LM1. The trait has been observed on both the external (enamel) and internal (dentine) surfaces; we only examined the enamel surface. In its strongest form (uninterrupted crest), it is present on the enamel surface in low to moderate (0–20 percent) frequencies on LM1 in *H. sapiens* (recent and fossil) as well as *Homo erectus*. It is less frequent on LM2 and LM3 (Wu and Turner 1993; this study). This contrasts the high frequency of this trait in *H. neanderthalensis* (80–100 percent) on all three molars (Bailey 2002a; this study). Martinón-Torres et al (2012) report similarly high frequencies for the middle trigonid crest on lower molars in the Sima de los Huesos material.On the basis of this, Bailey (2002a) concluded that *H. sapiens* preserves a primitive trait frequency, and the condition in *H. neanderthalensis* is derived.

A recent study of the middle trigonid crest on the dentine surface (EDJ) suggests the condition in *H. sapiens* may be derived as well. Bailey et al. (2011)

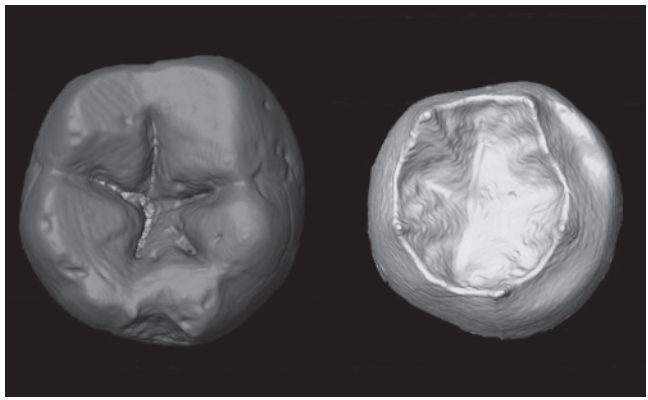

Figure 10.6. "Modern" morphology of the middle trigonid crest: it is completely absent on the enamel (left) and dentine (right) surfaces.

observed that the middle trigonid crest is *always* expressed in some form (ridges or complete crest) in the dentine of Neanderthals, *Australopithecus,* and *Pan*, regardless of the expression on the external tooth surface. In contrast, >50 percent of recent *H. sapiens* showed no expression of the middle trigonid crest at the EDJ. The dentine surfaces of *Homo erectus* and *H. heidelbergensis* (including Sima de los Huesos) molars have yet to be studied; however, on the basis of the strong correlation found between morphology at the enamel and dentine surfaces (Bailey et al. 2011; Skinner et al. 2008), we believe the molars of both groups will show some expression (ridges or complete crest) on the dentine surface. If true, then the absence of a middle trigonid crest on the dentine surface could be considered derived in *H. sapiens*, which appears in some of the earliest members of this species from Africa (Figure 10.6).

10.4.2 Some remarks about tooth size

While tooth size was not our focus, similarities between some postcanine morphological characters of *H. sapiens* and the *H. heidelbergensis* material from Sima de los Huesos warrant explanation. Recently, Gomez-Robles et al. (2012) used geometric morphometrics to examine the effect of allometry on crown shape of UM2 and UM3 in fossil and recent hominins. Differences in crown shape reflect cusp reduction as well as the concomitant reorientation of cusps that follows. The authors found small but significant allometric effects in both cases, with a stronger signal in UM3 than in UM2. As such, it is likely that hypocone reduction in *H. heidelbergensis* and *H. sapiens* can be partially explained by crown size reduction.

An assessment of allometry and crown shape has yet to be undertaken on the lower molars. Loss of the hypoconulid was the one lower molar character that seemed diagnostic of *H. sapiens,* yet it was also observed in the Sima de los Huesos material. To assess the relationship between crown size and hypoconulid loss, we subjected crown size and presence/absence data to Pearson's R test. This analysis could only be undertaken on the *H. sapiens* material since we do not have individual trait scores for the Sima de los Huesos material. Results suggest a moderate and significant ($r = .60$, $p < .05$) correlation between crown size and hypoconulid loss.

While a few recent studies examined the relationship between nonmetric dental traits and tooth size (Hunter et al. 2010; Kondo and Townsend 2006), no study has systematically studied the effect of dental reduction on morphology. Paradoxical relationships need to be clarified [e.g., larger teeth tend to have stronger expression of Carabelli's cusp (Kondo and Townsend 2006), but populations with the highest frequencies of this trait (Western Europeans) are also those with the smallest teeth]. Crown size may predict some aspects of dental morphology, but there is no simple relationship between the two. It is also probable that some traits are more "vulnerable" to crown reduction than others (for example, those in the distal portion of the tooth). It will be important for future studies to clarify and describe these relationships to distinguish homology and homoplasy in the dental fossil record.

10.5 Summary and conclusions

This chapter began with the question "What is it that makes us dentally modern?" We tried to answer this question by investigating the range of nonmetric dental variation in recent and fossil *H. sapiens* compared to that of non-*sapiens* fossil hominins. We found most dental nonmetric traits in *H. sapiens* are also present in non-*sapiens* hominins (e.g., shovel-shaped incisors, lower molar hypoconulid, and Y-5 dental pattern). Moreover, there are few dental traits that can be considered diagnostic of our lineage. Some seem to have evolved early in our lineage, such as (1) flat, featureless incisors; (2) symmetrical, rounded lower premolars with a single (or no) lingual cusp and U-shaped fissure pattern; and (3) lower molars lacking a middle trigonid crest (on enamel and dentine surfaces). Others appear to have evolved recently, for example, double-shoveled upper incisors. Certain traits that may have once been considered unique to our lineage (e.g., four-cusped LM1 and LM2, and three-cusped UM2) have been identified in some Middle Pleistocene hominins (Martinón-Torres et al. 2012), so these cannot be used to diagnose *H. sapiens* in a fossil context.

With the exception of double-shoveled incisors, the distinguishing features of *H. sapiens* dentitions involve crown simplification rather than complexity. With the discovery of the Middle Pleistocene dental collection from Sima de los Huesos, it appears that crown reduction can no longer be considered a unique *H. sapiens* trait (Bermúdez de Castro and Nicolas 1995). Considering the metric and morphological similarities between Sima de los Huesos molars and those of *H. sapiens,* future studies should elucidate relationships between crown size and morphological simplification. These findings are important in light of claims of very early *H. sapiens* in the fossil record (Hershkovitz et al. 2010), where greater emphasis has been placed on tooth size rather than morphology in the interpretation of these important fossils.

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11 *From outer to inner structural morphology in dental anthropology: integration of the third dimension in the visualization and quantitative analysis of fossil remains*

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11.1 Introduction

Dental remains usually represent the most common evidence testifying to the life of extinct taxa in a given region at a given moment. The appropriate assessment, safeguard, and exploitation of this unique heritage for research and educational purposes represent a crucial task for paleobiologists, museum curators, and teachers. However, by definition, the management of the fossil record is affected by its intrinsic characteristics of rarity, uniqueness, fragility, and heterogeneous dispersal. Also, while dental remains are characterized by a high mineral content, their handling for direct observation, analysis, reproduction, casting, and display is nonetheless risky. On the other hand, notably in the field of paleoanthropology, there is a growing demand for access to original specimens and collections for increasingly detailed investigations, as well as for public display. In fact, in parallel with results from research on mammal (including primate) dental developmental biology and quantitative genetics (e.g., Braga and Heuzé 2007; Harjunmaa et al. 2012; Hlusko and Mahaney 2007; Hlusko et al. 2004; Jernvall 2000; Jernvall and Jung 2000; Kangas et al. 2004; Mitsiadis and Smith 2006; Pereira et al. 2006; Rizk et al. 2008; Thesleff et al. 2001), advances in comparative tooth structural morphology and mesomicroanatomy of extant and extinct

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hominids show that a significant amount of valuable information for assessing their taxonomy, evolutionary pathways and phylogenetic relationships, sex- and age-related models of developmental timing and patterning (life history), ecorelated adaptive strategies and dynamics, seasonally related health conditions, chronogeographical trends in functional adaptation and fluctuating variation patterns lies "safely" stored inside crowns and roots (e.g., Bailey et al. 2011; Bondioli et al. 2010; Bromage et al. 2007; Dean 2006, 2010; Emonet et al. 2012; Grine et al. 2012; Guatelli-Steinberg 2009; Kelley and Schwartz 2012; Kono 2004; Kono et al. 2002; Kupczik and Dean 2008; Kupczik and Hublin 2010; Lacruz et al. 2008; Lee et al. 2010; Macchiarelli and Bailey 2007; Macchiarelli et al. 2008; Mahoney 2008; Olejniczak et al. 2008a; Schwartz and Dean 2008; Shimizu and Macho 2007; Skinner et al. 2008a, 2010; Smith 2006, 2008; Smith and Tafforeau 2008; Smith et al. 2005a, 2006a, 2008, 2012; Tafforeau and Smith 2008; Vogel et al. 2008; Zanolli et al. 2011). Nonetheless, beyond the usual noise resulting from taphonomic and diagenetic processes during the fossilization process, access to this precious information reservoir is a priori limited by the need to ensure the integrity of the specimens; this objective constraint allows only a limited use of invasive analytical approaches in the morphostructural and geochemical study of the dental fossil record (Beynon et al. 1998; Cerling et al. 2011; Copeland et al. 2011; Dean and Leakey 2004; Dean and Schrenk 2003; Dean et al. 1993, 2001; Grine et al. 2012; Lee-Thorp et al. 2010; Macchiarelli et al. 2006; Mahoney et al. 2007; Martin et al. 2003; Richards et al. 2008; Schwartz et al. 2003; Smith et al. 2003, 2005b, 2007a, 2009a; Sponheimer et al. 2006).

In response to the potentially conflicting requirements of safeguard versus exploitation of fossil teeth, available technologies allow high-resolution reproduction of any specimen; the new generation of noninvasive analytical tools developed in the domain of rheological sciences currently permits the extraction of a wide range of morphostructural information. When combined, these approaches assure "immortalization" of fossil specimens and their rendering for direct and/or virtual manipulation, assessment, exportation (see examples in Macchiarelli and Weniger 2011; Weber and Bookstein 2011; Zollikofer and Ponce de León 2005). In particular, the increasing use of analytical imaging techniques such as those based on microfocal X-ray computed tomography (microtomography) for the virtual exploration, extraction, "cleaning," and bi- (2-D) three-dimensional (3-D) rendering of the mesomicrostructural signature stored in mineralized tissues has disclosed recent and new promising perspectives in paleobiology (Mazurier et al. 2006; Smith and Hublin 2008; Tafforeau et al. 2006; Taquet 2010).

Following the pioneering applications of synchrotron radiation microtomography (SR-μCT) to the study of enamel microstructure in recent and fossil primates (Tafforeau 2004; see also Smith and Tafforeau 2008; Tafforeau and Smith

2008) and the first noninvasive 2-D–3-D virtual analyses of Mio-Pliocene fossil hominid (Kunimatsu et al. 2004; Rossi et al. 2004) and hominin (Macchiarelli et al. 2004) dental remains using industrial microtomography (μCT), the last few years have witnessed widespread imaging applications in dental (paleo) anthropology. Some researchers considered various methodological aspects and perspectives in the use of microtomographic-based analytical techniques to detail tooth morphology (e.g., Avishai et al. 2004; Benazzi et al. 2009, 2011a, b; Bondioli et al. 2010; Bunn et al. 2011; Olejniczak 2006; Olejniczak and Grine 2006; Olejniczak et al. 2007a, b; Suwa and Kono 2005; Tafforeau et al. 2012); others focused on the quantitative assessment of endostructural tooth variation in extant taxa/populations (e.g., Emonet et al. 2012; Feeney et al. 2010; Gantt et al. 2006; Kono 2004; Kono et al. 2002; Kupczik and Hublin 2010; Kupczik et al. 2009; Olejniczak 2006; Olejniczak et al. 2007a, 2008a; Skinner et al. 2008a, 2010; Smith et al. 2008; Suwa and Kono 2005; Tafforeau and Smith 2008). Today, an increasing number of applications include high-resolution virtual imaging to disclose the inner structure of fossil hominid/hominin dental remains (Braga et al. 2010; Brunet et al. 2005; Chaimanee et al. 2006; Emonet et al. 2012; Jaeger et al. 2011; Kunimatsu et al. 2004, 2007; Macchiarelli et al. 2004, 2008, 2009; Olejniczak et al. 2008b, c; Rossi et al. 2004; Skinner et al. 2008a, b, 2009; Smith et al. 2011; Suwa et al. 2007, 2009; Zanolli et al. 2010a). Together, these approaches have significantly helped in "recognizing and coping with homoplasy in and around the hominin clade" (Wood 2010: 8908). Within this framework, special attention has been devoted to comparative characterization of evolutionary changes within our genus (Bayle 2008; Bayle and Macchiarelli 2012; Bayle et al. 2009a, b, 2010, 2011, 2012; Benazzi et al. 2011a, c, d; Bermúdez de Castro et al. 2010; Crevecoeur et al. 2010; Kupczik and Hublin 2010; Macchiarelli et al. 2006, 2007, 2008; Olejniczak and Grine 2005; Olejniczak et al. 2008d; Prado-Símon et al. 2012a, b; Smith P. et al. 2006; Smith T.M. et al. 2006b, 2007a, b, 2009a, b, 2010, 2012; Toussaint et al. 2010; Zanolli et al. 2010b, 2012).

Though established less than 10 years ago, "virtual dental (paleo)anthropology" is already revealing its potential as a highly fertile domain of investigation, that is, a sharp "tool" capable of adding significant original evidence to traditional methods (Macchiarelli et al. 2008). This technological "transition" implies real innovation in paleomorphological studies: high-resolution 3-D versus traditional 2-D imaging and surface-volumetric versus linear quantitative characterization of the endostructural tooth variation. As a result, our approach expands from the "container," that is, outer morphology to the "contents" (Bayle et al. 2011). Nonetheless, a reliable container-to-contents investigative shift requires not only new techniques (and technologies), but: (1) fundamental new concepts concerning what, why, and how data should be extracted; and (2) quantitatively assessed analytical work dealing with high-resolution

virtual tooth imaging. From this perspective, long-term theoretical and methodological work is still needed.

Here we present three new examples illustrating, at different scales, the value of 3-D virtual rendering and characterization of the human dental fossil record in moving from the outer to inner morphology. The first case investigates antimeric variation in tooth structural organization in the lower dentition of a Neanderthal individual. The second covers the degree of parallelism between deciduous and permanent crowns in tracking taxon-related structural changes in tissue proportions of *Homo* over the last one million years. Finally, we show how fossil tooth roots can be virtually "unrolled" and compared for dentine thickness topographic variation. While these case studies provide original information about the "hidden evidence" (Macchiarelli and Bondioli 2005), they also reveal how poor our current state of knowledge is regarding the field of "virtual dental (paleo)anthropology."

11.2 Intraindividual antimeric variation in tooth tissue proportions: a Neanderthal case

In studies of recent humans, fluctuating versus directional odontometric asymmetry, among other markers (e.g., enamel hypoplasia), is often used as a measure of developmental (in)stability, to reflect the amount of relative stress a population experienced (Corruccini et al. 2005; Guatelli-Steinberg et al. 2006; Hoover et al. 2005). However, besides some qualitative remarks on antimeric variation in 3D root morphology (Kupczik and Hublin 2010) and root canal geometry (Prado-Símon et al. 2012a), no systematic quantitative assessment of endostructural asymmetry has been realized in complete fossil hominin/human dentitions. With reference to the enamel-dentine junction (EDJ), one notable exception is represented by study of the Sts 52 *Australopithecus africanus* postcanine dentition from Sterkfontein, South Africa (Braga et al. 2010).

Here we use the lower permanent dentition of Regourdou 1 to investigate antimeric variation in tooth tissue proportions. We then systematically compare our findings to the degree of dimensional asymmetry expressed at the outer crown by the buccolingual (B-L) diameter (data from Maureille et al. 2001), not affected by occlusal or interproximal wear.

Regourdou 1 is the partial skeleton of a young adult Neanderthal individual, likely from the OIS 4, discovered in 1957 at Montignac-sur-Vézère, near Lascaux, France; it was found in a buriallike context associated with La Quina type Mousterian artifacts (Madelaine et al. 2008). While lacking the cranium, Regourdou 1 preserves a virtually intact mandible with a fully erupted, moderately worn dentition (Figure 11.1A). We had the opportunity to scan 41

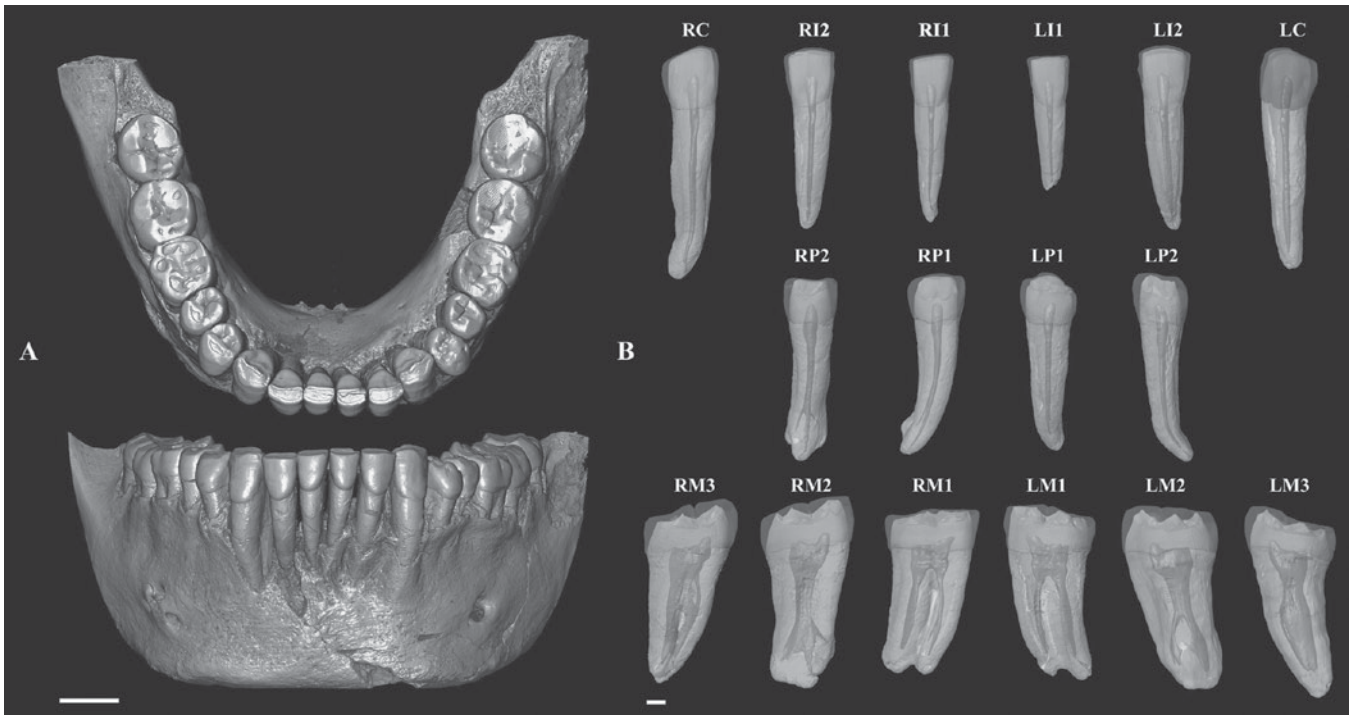

Figure 11.1. The lower dentition of the adult Neanderthal Regourdou 1. Image A shows the microtomographic-based 3D reconstruction of the mandible in occlusal (top) and frontal (bottom) views (scale bar, 1 cm). Image B shows the entire series of virtually extracted teeth (in labial/buccal view) rendered in transparency (scale bar, 2.5 mm). (Please see color plate section.)

bony elements from this individual at the beamline ID 17 of the European Synchrotron Radiation Facility (ESRF), Grenoble. Specifically, we detailed nineteen elements from the right side (i.e., eighteen total bones), fourteen from the left (twelve bones), and eight elements from the axial skeleton (seven bones). The entire dentition was scanned at a spatial resolution of 45.5 µm (Bayle et al. 2011; Macchiarelli et al. 2008).

Following standard procedures routinely applied for tooth volume virtual reconstruction and semiautomatic threshold-based segmentation (details in Bayle et al. 2009a, 2010; Olejniczak et al. 2008d; Zanolli et al. 2012), eleven linear, surface, and volumetric variables describing tooth structural organization and proportions were measured or calculated for each virtually extracted tooth (Figure 11.1B): volume of enamel cap (Ve; mm^3); total volume of dentine (Vd; mm^3); total volume of pulp (Vp; mm^3); total tooth volume (Vt; mm^3); volume of crown dentine (Vcd; mm^3); volume of crown pulp (Vcp; mm^3); volume of crown dentine + pulp (Vcdp; mm^3); surface area of enamel-dentine junction (SEDJ; mm^2); percent of crown volume that is dentine and pulp (Vcdp/Vc %); three-dimensional average enamel thickness (3D AET; mm); and the scale-free three-dimensional relative enamel thickness (3D RET). Because of its apical break, Ve, Vp, and Vt were not assessed on the left central incisor. For each variable, asymmetry was calculated following Corruccini et al. (2005) and transformed into a percent value. Results are summarized in Table 11.1.

Overall, with the exception of LP2 (−8.5 percent), outer crown linear asymmetry is low (range: 0.2–2.9 percent); the right (R) antimere is almost systematically larger (7/8 cases). However, the situation is more varied when moving inward (i.e., R > L is found in ca. 64 percent of cases), and dental wear must be taken into account as an additional factor for possible developmental noise.

Regourdou 1 shows moderate attrition, but occlusal wear on the incisors and canines is more marked than on the premolars and molars – a feature typical of Neanderthals (Volpato et al. 2012). For the present analysis, we rendered occlusal wear via 3D topographic mapping of site-specific enamel thickness variation by initially using a chromatic scale where thickness increases from dark blue to red; these colors are, by necessity, converted to black and medium gray, respectively, in the halftone image (Figure 11.2). While wear is uniformly distributed on the anterior teeth (low fluctuating asymmetry for Ve, 3-D AET, and 3D RET), variation is evident in the postcanine dentition. Most notable are the LP1s, where asymmetry for volume of the enamel cap (Ve) reaches −47.7 percent because of the more worn left crown (Figure 11.2B); moreover, obvious antimeric differences affect the LM1s (18.7 percent) and LM3s (−19.7 percent). Interestingly, in addition to evidence from the wear-dependent 3D AET and 3D RET variables, LP1 is the most asymmetric tooth for four additional values describing inner structural organization (Vcd, Vcdp,

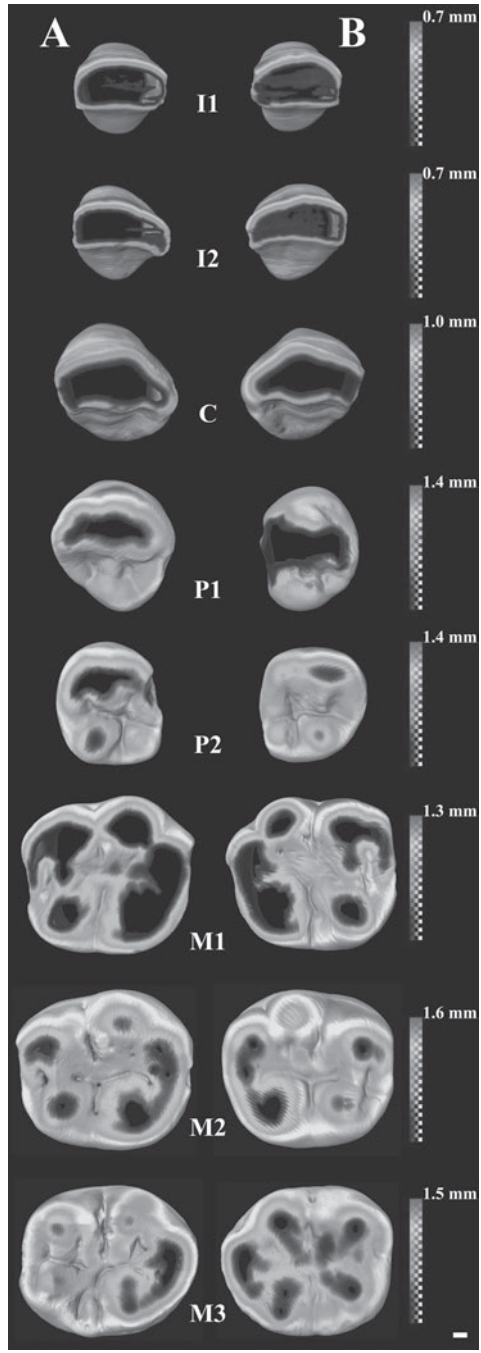

Figure 11.2. Regourdou 1. Comparative enamel thickness cartographies of the virtually reconstructed right (A) and left (B) lower tooth crowns in occlusal view. Topographic variation is rendered by a tooth-specific thickness-related scale (original version in pseudocolors) ranging from dark gray (relatively thin to entirely removed enamel) through light gray (relatively thicker enamel). Scale bar, 1 mm. (Please see color plate section.)

SEDJ, %Vcdp/Vc); it also displays the second highest value for volume of the crown pulp (Vcp: −26.4 percent). In this respect, marked asymmetry at the enamel-dentine junction level is uniquely expressed in this tooth (SEDJ P1: −22.4 percent); values for the other teeth range between −2.5 percent (P2) and 10.8 percent (M1) (Table 11.1).

The discrepancy in occlusal wear between the two LP2s is less than that of the LP1s (low asymmetry for Ve, 3D AET, and 3D RET); further, two slightly larger dentine spots are present on the right crown, which even shows a distal enamel break (Figure 11.2A). In any event, as noted for the BL-diameter, the right antimere shows the highest value for Vp (−22.4 percent). The associated value of −17.9 percent for total volume of the dentine (Vd) is not entirely ascribable to differential formation of secondary dentine that similarly affects the right LP2. Conversely, the pattern for most inner variables of the M3s (where asymmetry for Vcp reaches −35.4 percent) is compatible with the greater wear on the left crown. Finally, it should be noted that antimeric variation in Regourdou 1, based on a variable often used to characterize endostructural tooth organization, that is, percent of crown volume that is dentine and pulp (Vcdp/Vc %), is clearly fluctuating and globally modest (range: 0.7–10.7 percent); it corresponds in 5/8 cases to the measurement error reported for such variables in tests of intra- and interobserver accuracy (Macchiarelli et al. 2008).

In sum, analysis of this single fossil reveals the need for additional, extensive research on the occurrence, polarity, possible meaning (functional/compensatory vs. developmental), and impact of intraindividual antimeric variation in tooth tissue proportions; the latter could be relevant in assessing intertaxon differences.

11.3 Evolutionary changes in human tooth tissue proportions: deciduous versus permanent signatures

Global evolutionary trends and patterns of chronogeographic variation in human tooth structural organization and tissue proportions have been poorly investigated to date. An attempt to model enamel thickness variation (2D AET and 2D RET) comparatively using 150 fossil *Homo* teeth spanning the last two million years (Smith et al. 2012) did not reveal any predictable pattern, nor clarify why crown size reduction from fossil to recent *H. sapiens* resulted from a greater diminution in coronal dentine than enamel. Of course, the lack of data from many samples representing key ecogeographic areas and evolutionary grades, largely due to logistical constraints in using advanced technologies to study the fossil record, is the primary issue responsible for our lack of knowledge. Additionally, an increasing amount of information is now available for

Table 11.1. *The lower dentition of the adult Neanderthal Regourdou 1. Percent of asymmetry (antimeric variation) assessed for a set of outer and inner linear, surface, and volumetric tooth variables and dental tissue proportions*

Tooth		B-L (mm)	Ve (mm^3)	Vd (mm^3)	Vp (mm^3)	Vt (mm^3)	Vcd (mm^3)	Vcp (mm^3)	Vcdp (mm^3)	SEDJ (mm^2)	Vcdp/Vc (%)	3D AET (mm)	3D RET
I1	left	6.99	27.38	–	–	–	69.23	1.86	71.09	81.7	72.19	0.34	8.09
	right	7.03	27.95	340.57	14.6	383.12	72.35	2.15	74.5	79.5	72.72	0.35	8.36
	% asymm.	–0.6	–2.1	–	–	–	–4.4	–14.5	–4.7	2.7	*–0.7*	–2.9	–3.3
I2	left	7.82	38.17	459.77	22.03	519.97	88.02	3.65	91.67	101.11	70.60	0.38	8.37
	right	7.86	38.81	467.2	20	526.01	86.76	3.2	89.96	97.68	69.86	0.4	8.87
	% asymm.	–0.5	–1.7	*–1.6*	9.7	*–1.2*	1.4	13.1	1.9	3.5	1.1	–5.1	–5.8
C	left	9.34	68.12	762.18	42.51	872.82	144.91	6.24	151.15	133.52	68.93	0.51	9.58
	right	9.61	66.66	786.25	39.66	892.58	138.92	5.61	144.53	129.5	68.44	0.51	9.81
	% asymm.	–2.9	2.2	–3.1	*6.9*	–2.2	4.2	10.6	4.5	3.1	0.7	*0.0*	*–2.4*
P1	left	8.96	52.87	563.87	22.93	639.67	109.54	2.83	112.38	94.13	68.01	0.56	11.64
	right	9.19	86.01	592.41	26	704.42	131.46	3.69	135.15	117.85	61.11	0.73	14.22
	% asymm.	–2.5	**–47.7**	–4.9	–12.6	–9.6	**–18.2**	–26.4	**–18.4**	**–22.4**	**10.7**	**–26.4**	**–20.0**
P2	left	8.12	87.59	482.39	24.15	594.12	109.06	3.35	112.41	111.31	56.21	0.79	16.3
	right	8.84	86.42	577.18	30.23	693.83	115.69	3.84	119.53	114.09	58.04	0.76	15.38
	% asymm.	**–8.5**	*1.3*	**–17.9**	**–22.4**	**–15.5**	–5.9	–13.6	–6.1	*–2.5*	–3.2	3.9	5.8
M1	left	10.37	119.58	1001.63	75.13	1196.34	276.24	8.67	284.91	201.46	70.44	0.59	9.02
	right	10.44	99.17	1047.44	64.98	1211.6	280.42	7.75	288.17	180.79	74.40	0.55	8.3
	% asymm.	–0.7	18.7	–4.5	14.5	–1.3	–1.5	11.2	*–1.1*	10.8	–5.5	7.0	8.3
M2	left	11.03	171.34	1133.02	87.87	1392.23	286.98	7.46	294.44	195.3	63.21	0.88	13.19
	right	11.05	157.61	1187.78	103.84	1449.23	290.8	7.83	298.63	202.81	65.45	0.78	11.63
	% asymm.	*–0.2*	8.4	–4.7	–16.7	–4.0	*–1.3*	*–4.8*	–1.4	–3.8	–3.5	12.1	12.6
M3	left	10.87	140.28	983.19	89.41	1212.88	247.43	6.03	253.46	179.9	64.37	0.78	12.32
	right	10.74	171.01	930.34	81.29	1182.63	251.48	8.62	260.1	193.68	60.33	0.88	13.83
	% asymm.	1.2	–19.7	5.5	9.5	2.5	–1.6	**–35.4**	–2.6	–7.4	6.5	–12.1	–11.6

Note: See the text for the meaning of the variables. 3-D RET is a scale-free estimate. Percent asymmetry is calculated as (L−R)/([L+R] * 0.5) (Corruccini et al. 2005). Negative values indicate right dominance; italics and bold indicate the lowest and the highest values, respectively. Note that the distal root of the left I1 of Regourdou 1 is missing.

the secondary dentition of several fossil human taxa (Smith et al. 2012); however, with few exceptions (Bermúdez de Castro et al. 2010; Macchiarelli et al. 2006; Zanolli 2011; Zanolli et al. 2010b, 2012), the endostructural condition of deciduous teeth is unreported for Early and Middle Pleistocene human specimens/samples. Some evidence suggests deciduous versus permanent molar enamel thickness distribution and relative proportions vary among extant and fossil hominid taxa (Macchiarelli et al. 2009). Inner signatures extracted from the primary and secondary dentition, respectively, may or may not provide similar/comparable pictures of time-related intrataxic evolutionary changes in tooth tissue proportions; this could be relevant when planning future analytical strategies in "virtual dental (paleo)anthropology."

Here we use published and original microtomographic-based data to compare, for the first time, subtle endostructural organization in several poorly to moderately worn deciduous and permanent molar crowns from (1) Javanese *H. erectus* (HEJ; Lm2 crown PCG.2 (Zanolli et al. 2012) and unpublished LM2/3 crown NG92 D6 ZE 57s/d 76 (cf. Zanolli 2011) from late Early to early Middle Pleistocene deposits of the Sangiran Dome); (2) early *H. heidelbergensis* from North Africa (HHNA; the isolated Um2 crown (Zanolli et al. 2010b) and unpublished LM3 virtually extracted from the mandible Tighenif 2, both from the early Middle Pleistocene site of Tighenif, Algeria); (3) later European *H. heidelbergensis* (HHE; unpublished Lm2 Arago 5 and rather worn LM3 Arago 106 crowns from the Middle Pleistocene Caune de l'Arago at Tautavel, France (Schwartz and Tattersall 2002: 41–53); and (4) European Neanderthals (NEA; six Lm2s from La Chaise-de-Vouthon and Roc de Marsal [Bayle et al. 2009a, b, 2010, 2011; Nespos Database 2011] and six LM3 from Krapina and Regourdou 1 [Bayle et al. 2011; Macchiarelli et al. 2008; Nespos Database 2011]). The extant human condition (EH) is represented by six Lm2 and six LM3 unworn crowns from a recent European sample (Bayle 2008; Bayle et al. 2010; and original data). Given the exploratory nature of this study, the mix of tooth types simply reflects the availability in our files of high-resolution microtomographic records.

To reduce the impact of crown size differences, we used the percent of crown volume that is dentine and pulp (Vcdp/Vc %) and the scale-free three-dimensional relative enamel thickness (3-D RET) (see previous section). Complementary to 3-D RET, we also used the 3-D RET of the lateral enamel only to avoid the problem of occlusal wear (Toussaint et al. 2010). Finally, to get an even approximate indication of signal polarity and coherence, we calculated the relative deciduous/permanent ratio for each variable.

After segmentation and volumetric assessment of the outer and inner structures, virtual renderings of selected deciduous (A) and permanent (B) molar crowns were produced (Figure 11.3); quantitative results are summarized in

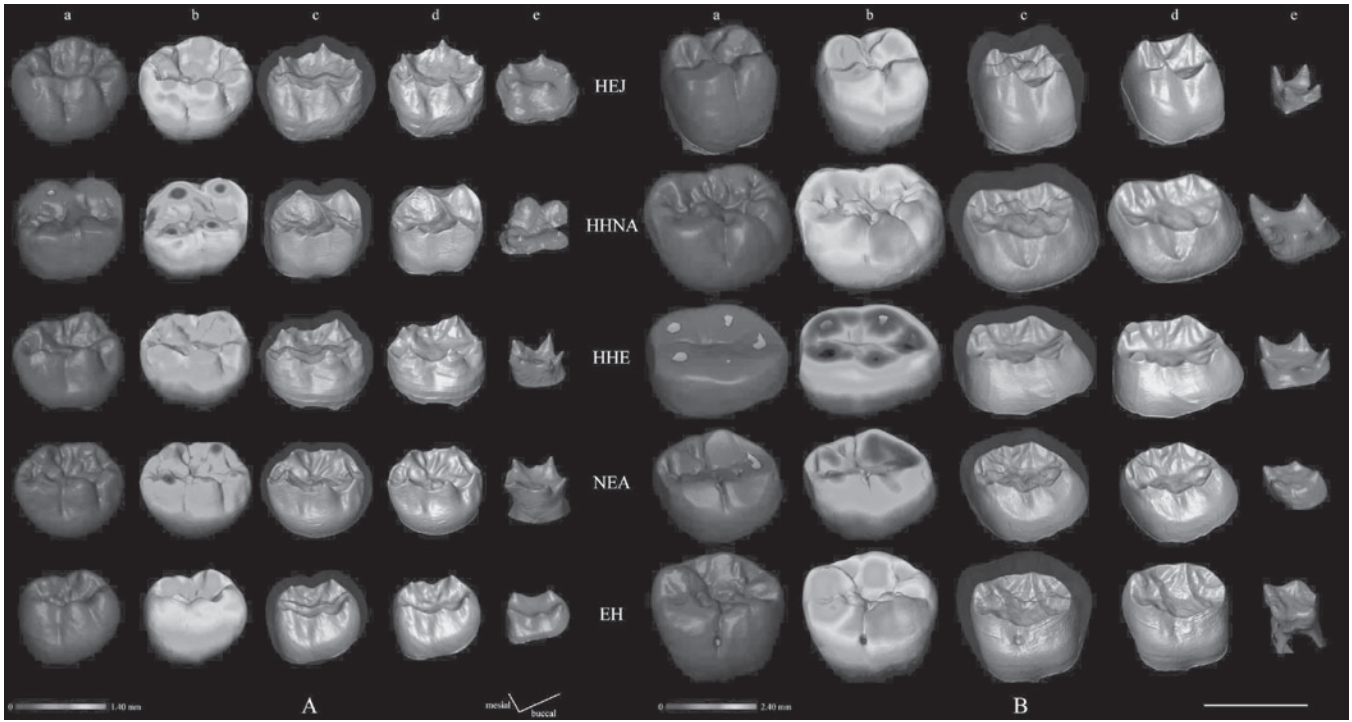

Figure 11.3. Microtomographic-based virtual rendering in occlusal-buccal view of the outer crown (a); the enamel thickness variation (b); the enamel-dentine junction (EDJ) with the enamel in semi-transparency (c); the EDJ (d); and the pulp cavity (e) (original version in pseudocolors) comparatively provided in deciduous (A) and permanent (B) molar crowns representing five fossil and extant human taxa/populations. In (b), topographic variation is rendered by a thickness-related scale ranging from dark gray (relatively thin to entirely removed enamel) through light gray (relatively thicker enamel). EH: extant humans; HEJ: *H. erectus* from Java; HHE: European late *H. heidelbergensis*; HHNA: early *H. heidelbergensis* from North Africa; NEA: European Neanderthals. See the text for details on the composition of the samples. Scale bar, 1 cm. (Please see color plate section.)

Table 11.2. *Evolutionary trends in human inner tooth structural organization. Degree of congruence (intertooth ratio) between the signals provided for the percent of the crown volume that is dentine and pulp (Vcdp/Vc %) and the three-dimensional relative enamel thickness (3-D RET and lateral 3-D RET) by deciduous and permanent molars representing five fossil and extant human taxa/populations*

Sample	Tooth (N)	Vcdp/Vc (%)	3-D RET	lateral 3-D RET
HEJ	Lm2 (1)	56.76	13.46	9.18
	LM2/3 (1)	51.06	18.98	8.55
	Lm2/LM3	**1.11**	**0.71**	**1.07**
HHNA	Um2 (1)	61.98	11.71	8.09
	LM3 (1)	49.95	20.27	9.57
	Um2/LM3	**1.24**	**0.58**	**0.85**
HHE	Lm2 (1)	60.88	11.58	7.62
	LM3 (1)	62.05	12.33	9.40
	Lm2/LM3	**0.98**	**0.94**	**0.81**
NEA	Lm2 (6)	66.17	10.03	6.90
	range	*63.96–67.76*	*9.49–10.92*	*6.47–7.58*
	LM3 (6)	53.75	17.25	9.59
	range	*47.19–64.10*	*10.96–21.77*	*6.28–10.35*
	Lm2/LM3	**1.23**	**0.58**	**0.72**
	range	*1.00–1.44*	*0.44–1.00*	*0.63–1.21*
EH	Lm2 (6)	59.70	14.08	8.69
	range	*52.04–64.89*	*11.98–18.93*	*6.58–11.47*
	LM3 (6)	50.39	19.19	8.82
	range	*45.22–53.15*	*17.78–20.89*	*6.28–10.35*
	Lm2/LM3	**1.18**	**0.73**	**0.99**
	range	*0.98–1.43*	*0.57–1.06*	*0.64–1.83*

Note: EH: extant humans; HEJ: *H. erectus* from Java; HHE: European late *H. heidelbergensis*; HHNA: early *H. heidelbergensis* from North Africa; NEA: European Neanderthals. See the text for the meaning of the variables and details on the composition of the samples. The intertooth ratios are given in bold.

Table 11.2. Compared to their permanent counterparts, deciduous molars systematically show a proportionally larger crown portion that is dentine and pulp, most notably in *H. heidelbergensis* from Tighenif and the European Neanderthal sample (average value); the remaining values are closer to the unit, with no obvious evidence of a time/taxon-related trend. As evidenced by the total 3-D RET, enamel is proportionally thicker in the permanent molars. The most contrasted signal is again provided by the early Middle Pleistocene North African sample and Neanderthals (but see later discussion). Interestingly, the figures for both Vcdp/Vc and total 3-D RET in North African and European

H. heidelbergensis differ; the former basically expresses a structural condition closer to that of Neanderthals. In this context, after removal of the problematically worn occlusal enamel (most notably the permanent molar from Tautavel), the only distinct trend is decreasing values for the lateral 3-D RET in deciduous molars from early to later *H. heidelbergensis* to Neanderthals. As a whole for deciduous and permanent molars, the closest fit to the modern human endostructural organization in terms of tissue proportions is *H. erectus*.

The variation in deciduous/permanent ratios expressed by the Neanderthal and extant human samples virtually encompasses that globally expressed by Javanese *H. erectus* and North African–European *H. heidelbergensis*. However, together with the unavoidable heterogeneity of intertooth contrasts in this analysis, our approach did not consider the likely effects of crown size reduction through the Pleistocene to early Holocene (e.g., Calcagno 1989; Frayer 1978; for a review, see Fitzgerald and Hillson 2008), which could influence the Vcdp/Vc ratio. Other factors not considered include (1) evidence for a positive allometric relationship between sizes of the dentine core and enamel cap in the deciduous molars; these variables have a negative allometric relationship among permanent molars (Grine 2005); or (2) the topographic variation reported in molar enamel thickness distribution (e.g., Kono 2004; Kono et al. 2002; Mahoney 2010; Smith et al. 2008). Accordingly, besides the need for more coherent intertooth contrasts, the likelihood at population/taxon level of such preliminary results requires confirmation using larger, more varied samples; this task represents a major challenge in the future development of "virtual dental (paleo)anthropology" and where morphometric assessment of the enamel-dentine junction will be likely pivotal.

11.4 Dentine topography and "unrolled" fossil roots

External root morphology reflects dietary adaptations as well as tooth use (e.g., Kovacs 1971; Kupczik and Dean 2008). For instance, hard-object feeders among primates have larger root surfaces than those feeding on softer objects (Kupczik and Dean 2008). In *Homo*, some differences in external mandibular molar root morphology (volume proportions, occurrence of pyramidal roots, metameric root surface area variation) among Neanderthals, Late Pleistocene anatomically modern, and recent humans have been linked to distinct occlusal loading regimes (e.g., Kupczik and Hublin 2010). However, site-specific topographic variation in internal root structure of the anterior human dentition has not yet been precisely quantified; this deficiency is related to objective methodological constraints, and the differential biomechanical impact of distinct masticatory and paramasticatory activities remains to be evaluated (Bayle et al. 2011).

The 2-D visualization on morphometric maps (MMs) of local morphometric properties of 3-D biological structures is usually performed by casting their properties on the surface of Euclidean bodies that could approximate their shape (Amtmann and Schmitt 1968; Bondioli et al. 2010; Jungers and Minns 1979; Morimoto et al. 2011; Zollikofer and Ponce de León 2001). For example, the MM of a femoral diaphysis is generated through projection of its (μ)CT-based original data into a cylinder, the closest fit to its 3-D shape (Bondioli et al. 2010; Morimoto et al. 2011; Zollikofer and Ponce de León 2001). However, because the shape of human tooth roots basically deviates from a regular reference form such as a cone, the degree of deformation during the projection phase of the MM algorithm may be unacceptable. Accordingly, a heuristic, though more precise alternative has been introduced to address "irregular" shapes (Bondioli et al. 2010).

Specifically, the MM is generated by direct measure of the investigated property (here, dentine thickness) on a finite number of planes virtually cutting orthogonally the original biological structure, that is, the root (Figure 11.4). That is, mapping proceeds by cross-sectioning the object in *n* equally-spaced slices at levels $Z_1 \ldots Z_n$ (Figures 11.4A–11.4B). In the case of a root, two concentric irregular polygons, representing the outer and the inner surfaces, are then calculated for each cross section. A cutting line is defined on the object surface and will represent the starting point of the unrolling procedure. To measure site-specific thickness variation, a set of lines are drawn at k equally-spaced angles ($d_1 \ldots d_k$) from the centroid of the section (Figure 11.4B), where the sum of the k angles equals 360°. For each angle, thickness is calculated as the segment length of the intersection of the line with the inner and the outer polygons. For each level Z_i it is then possible to derive a vector S_i of thickness $s_{i,j,}$ where $j = 1 \ldots k$ and k are the sampling angles (Figure 11.4C) and to visualize in graphic form the variation obtained for the n cross sections (Figure 11.4D).

The object's surface is virtually unrolled starting from the cutting line: N = nk bidimensional XY coordinates are assigned to each elements $s_{i,j}$ of the vectors $S_1 \ldots_n$, where $Y_{i,j}$ represents the Z_i level value, and it is the same for all the $j = 1 \ldots k$ elements of the vector S_i, and $X_{i,j}$ is calculated as the portion of the perimeter on the outer surface from the cutting plane to the j-th angle. The X coordinates of the S vectors are then normalized so the midpoint of each vector assumes a 0 value. For this kind of map, geostatistics-derived tools, like ordinary kriging (Pebesma 2004), are used to estimate the standardized thickness at intersection points of the regularly spaced grid. The MM is then rendered using a pseudocolor scale that renders relative values of thickness (shown as various shades of gray in the Figure 11.4E halftone).

Compared to a classical approach, this procedure generates a planar map with irregular borders that strictly relates to the original 3-D shape. As a whole, it reflects more accurately the original thickness distribution of the dentine

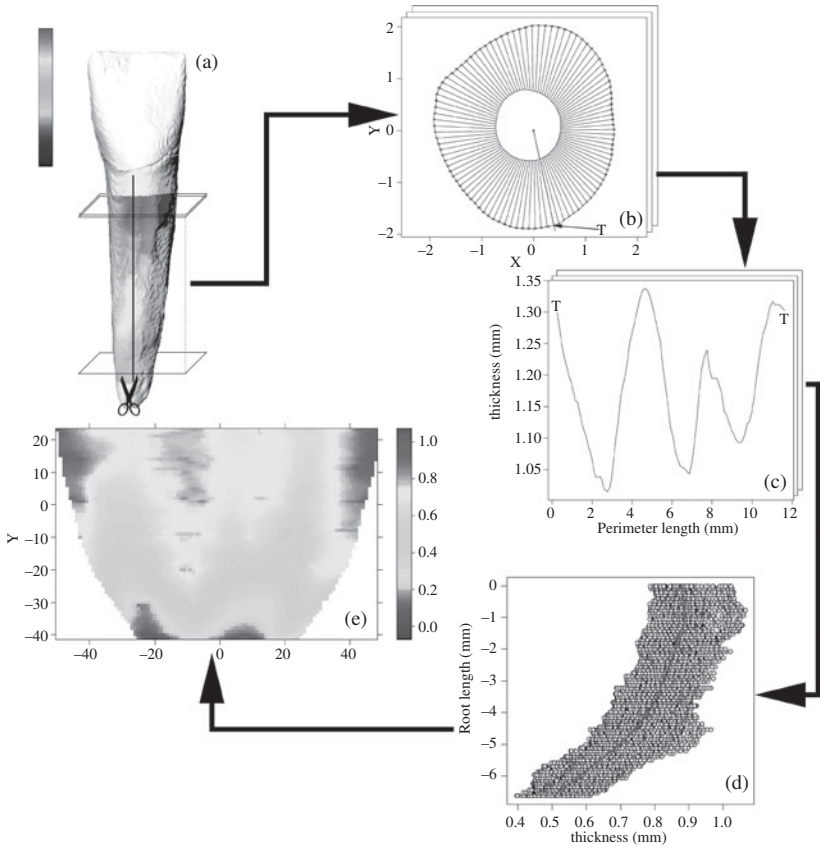

Figure 11.4. Schematic representation of the process of morphometric map (MM) generation specifically adapted to irregularly shaped 3D structures such as tooth roots. (a) Microtomographic-based rendering of a human deciduous incisor (lingual view) showing dentine thickness variation. The vertical line represents the cutting edge for root unrolling. (b) Virtual cross section of the root at a generic level Z_i, where X and Y are the original coordinates of the translated surface with the origin set at the centroid, and T indicates the cutting point. (c) Profile of dentine thickness variation at Z_i level. (d) Dentine thickness variation expressed through the $Z_1 \ldots Z_n$ entire set of virtual cross sections (the line indicates the mean values). (e) The MM of the virtually unrolled root showing dentine thickness topographic variation. In A and E, variation is rendered by a thickness-related scale (original version in pseudocolors). In E, the darker areas appearing near the bottom and those obliquely/vertically oriented in the middle-superior part of the map, respectively, correspond to the thinnest and the thickest regions, the remaining light gray areas indicating intermediate values. (Please see color plate section.)

tooth root and is useful for independent characterization of unique specimens. However, since this approach limits the possibility of standardization (i.e., different specimens provide maps of different shapes), the value of related statistical comparisons among variably sized objects is diminished.

In practical terms, after threshold-based segmentation of the original μCT record and surface rendering of the root components (dentine and pulp chamber), creation and analysis of the synthetic MM illustrating dentine topographic variation involve three distinctive phases: (1) 3-D dentine thickness assessment, (2) mapping the external surface into a plane, and (3) standardization (Bondioli et al. 2010). Accordingly, the roots are virtually unzipped vertically along the middle of their lingual aspect and then unrolled.

On the basis of their high-resolution microtomographic record, we used MM techniques to assess variation in dentine thickness topography of deciduous incisors and canines from Neanderthals, Upper Paleolithic, and recent humans comparatively. Specifically, we compared consensus maps summarizing extant human figures (EH) to structural signatures virtually extracted from the following fossil specimens: S14–2 (Li1), S14–3 (Li2), and S45 (Lc) from La Chaise-de-Vouthon abri Suard (Bayle et al. 2010, 2011; Macchiarelli et al. 2007) and the lower anterior arcade of the infant from Roc de Marsal (Bayle et al. 2009a, 2011); all Neanderthals; and that from the Gravettian child of Lagar Velho (Bayle et al. 2010, 2011). For the specific purposes of this exploratory study, we restricted the region of interest and arbitrarily represented dentine thickness variation in the interval between 50 and 85 percent of the total root length (where 85 percent is toward the tooth cervix).

The comparative MMs are shown in Figure 11.5. Overall similarities in the patterns of dentine thickness distribution are found among all specimens for each tooth-specific root; however, the fossil specimens evidence localized contrasts, notably near the cementoenamel junction. Although the available samples do not allow for any conclusive statements, it appears that the most highly contrasted maps characterize the Neanderthal roots of both lower deciduous incisors. In this context, it is noteworthy that the Gravettian child from Lagar Velho exhibits intermediate thickness (cf. Bayle et al. 2011).

Differences in molar root extension rates between Neanderthals and modern humans suggest that various developmental mechanisms likely acted on root formation, leading to different structures (Kupczik and Hublin 2010; Macchiarelli et al. 2006). This finding may also be applicable to the anterior dentition, though no data are currently available on root extension rate in Neanderthal incisors and canines.

These preliminary results support the use of virtual cartography as a valuable tool for quantifying, longitudinally and transversely in one image, the asymmetric distribution of tooth root dentine thickness in fossils. Accordingly, the perspective for comparing root architectures among more diverse hominin dentitions adapted to a range of diets may reveal whether internal root architecture responds to loading and directional stresses/strains in a predictable way like that in external morphology (Kupczik and Dean 2008; Kupczik and Hublin 2010).

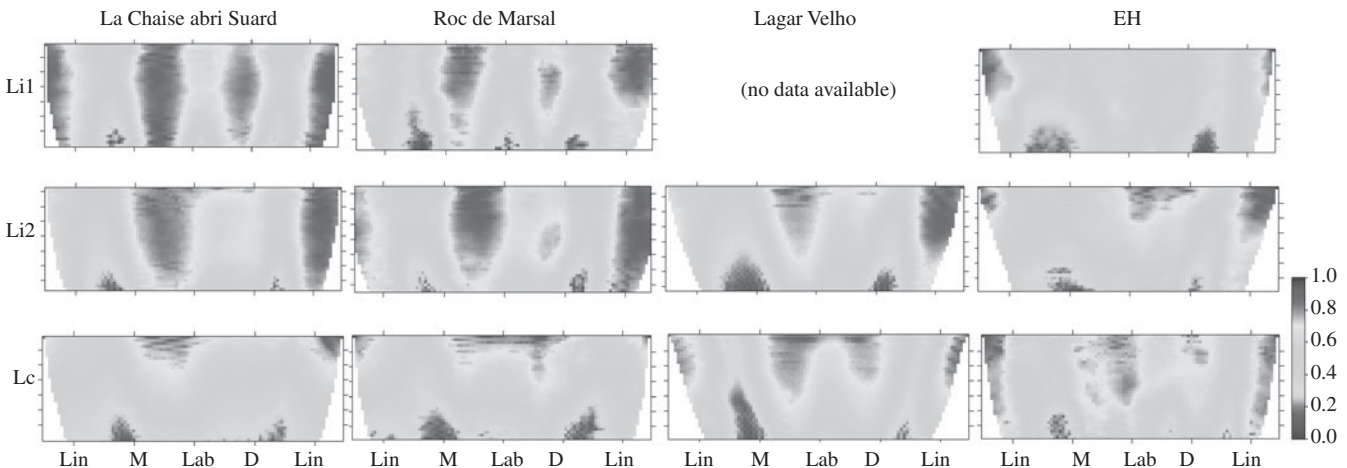

Figure 11.5. Comparative standardized morphometric maps (MMs) of virtually unrolled tooth roots (portion 50–85 percent of the total root length, where 85 percent [upper] is toward the tooth cervix) of lower deciduous incisors (Li1 and Li2) and canines (Lc) from two Neanderthal specimens (La Chaise abri Suard and Roc de Marsal), the Upper Paleolithic (Gravettian) child from Lagar Velho, and extant humans (EH, consensus maps). Dentine topographic variation is rendered by a thickness-related scale (original version in pseudocolors). In all cases, the darker areas appearing near the bottom and those obliquely/vertically oriented in the middle-superior part of the maps, respectively, correspond to the thinnest and the thickest regions, the remaining light gray areas indicating intermediate values. Lin: lingual; M: mesial; Lab: labial; D: distal. (Please see color plate section.)

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12 *Afridonty: the "Sub-Saharan African Dental Complex" revisited*

JOEL D. IRISH

12.1 Introduction

As the title implies, this chapter revisits earlier research on African dental morphology. Specifically, the focus here, in light of newly recorded data, is to reassess the validity and utility of the "Sub-Saharan African Dental Complex" (SSADC) (Irish 1997). In the spirit of previous attempts at global categorization (e.g., Hanihara 1968; Turner 1987), the SSADC was intended to epitomize commonalities observed in the subcontinent's diverse inhabitants. A reassessment is also timely, given the apparent misgivings of some in this volume concerning the practice.

In 1993, I proposed that frequencies of certain nonmetric features of the permanent crowns and roots provide an overall dental characterization of Africans. Specifically, nine high- and two low-frequency traits clearly differentiate sub-Saharan peoples from North Africans (Irish 1997), Europeans, Southeast Asian Sundadonts, Northeast Asian/New World Sinodonts, Australians, and Melanesians (Turner 1987, 1992a). In this instance "high" and "low" do not refer to absolute frequencies, but instead are relative to those expressed by other world samples. Therefore, this suite of 11 traits, that is, the SSADC (Irish 1997), includes the highest occurrences of (1) UC Bushman canine, (2) two-rooted UP1, (3) UM1 Carabelli's "trait" (i.e., the full range of expression from pit through large cusp on mesiolingual surface), (4) three-rooted UM2, (5) LM2 Y-groove pattern, (6) LM1 cusp 7, (7) LP1 Tome's root, (8) two-rooted LM2, and (9) UM3 presence, along with the lowest frequencies of (10) UI1 double shoveling and (11) UM1 enamel extensions. The SSADC was based on pooling several spatially diverse and largely synchronic (i.e., nineteenth–early twentieth centuries) samples (Irish 1997); as such, it was intended as a preliminary characterization. Nevertheless, the SSADC helped

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"place" sub-Saharan peoples on a global scale for tooth crown and root morphology and proved useful for biological affinity studies in samples [including a better understanding of human origins (discussed later)], and forensic applications in individuals (Irish in press).

12.2 The dental place of sub-Saharan Africans in the world

Subsequent to defining the SSADC, additional dental data were published on samples from around the world (Lipschultz 1996; Scott and Turner 1997). These data, like mine, were recorded using the Arizona State University Dental Anthropology System (ASUDAS), which is described elsewhere in this volume (also Scott and Turner 1997; Turner et al. 1991). Of these data, 21 ASUDAS traits in 13 pooled comparative samples were used to facilitate a more comprehensive dental characterization of Africans. Details are provided in Irish and Guatelli-Steinberg (2003), along with descriptions of African fossil hominin samples to which the modern material were also compared. In brief, a multivariate distance statistic, that is, the mean measure of divergence (MMD) (Green and Suchey 1976; Sjøvold 1973, 1977), and principal components analysis (PCA) based on all trait frequencies yielded nearly identical information about intersample variation.

This variation, sans hominin samples from the 2003 article, is illustrated in a plot of the first two principal components (Figure 12.1); more than 80 percent of the variance is accounted for on the two axes. Three broad geographic-based groups are evident: (1) Europe/Mediterranean (Europe, West Asia, North Africa), (2) Northeast Asia/New World (South Siberia, China-Mongolia, Northeast Asia, American Arctic, North and South Native Americans), and (3) Australia/Oceania (Southeast Asia, Australia, Melanesia, Micronesia, Polynesia). These groupings, alone, support the utility of categorization at a broad, that is, geographic, level [e.g., Mongoloid Dental Complex (Hanihara 1968) and Sinodonty characterize the second grouping]. Moreover, the Southeast Asian sample, as would be expected given known population history, is intermediate between the latter two groups.

The sub-Saharan sample is divergent from all others, though it is more or less equidistant between Europe/Mediterranean and Australia/Oceania. Again, known population (pre)history can account for the former association. Any similarity to the latter group may seem unlikely, but it is not anomalous. Many researchers have found seeming skeletal and genetic links among the peoples of these broad geographic regions (discussed in Irish 1993, 1997; Hanihara Chapter 19, this volume). Cavalli-Sforza and colleagues (1996) even suggested that after 60,000 BP, Africans developed seagoing skills that allowed

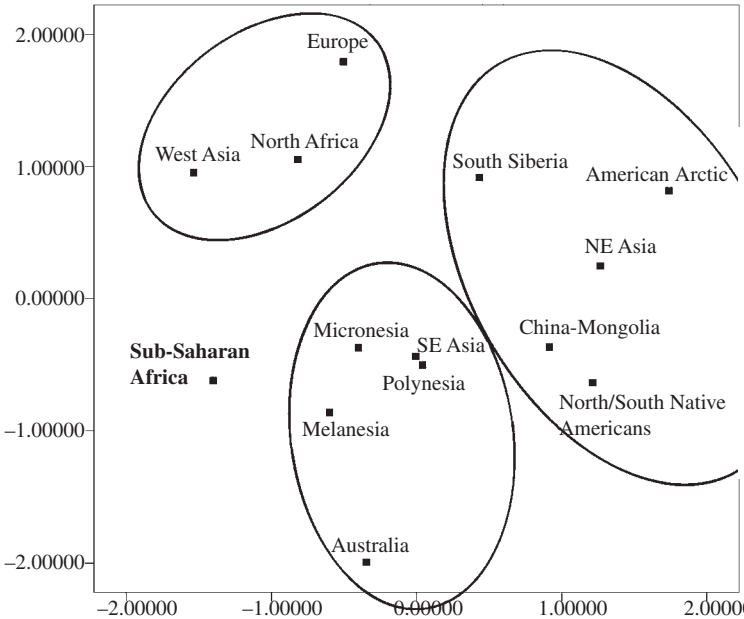

Figure 12.1. Scatterplot of the first two principal components among the pooled sub-Saharan African and comparative world dental samples. Accounts for >80 percent of the total variance. See text for details.

them to contact Australia. The sub-Saharan sample is least like the Sinodonts of Northeast Asia/New World, who are at "opposite ends of a dental morphological spectrum" (Irish 1997:462). This divergence is illustrated in a bar graph (Figure 12.2) of SSADC trait presence in the sub-Saharan Africans and a combined Sinodont sample [i.e., group 2 (discussed earlier), using matching ASUDAS breakpoints (refer to Table 12.1 later) based on data from Turner (1985)].

12.3 Origins of key sub-Saharan African dental traits

While initially assessing their derivation, I observed that the high- and low-frequency traits of the SSADC are often present or absent, respectively, in extinct and extant hominoids and fossil hominins (Irish 1993, 1997, 1998a). Confirmatory references include Gregory (1922), Gregory and Hellman (1926), Weidenreich (1937), Schultz (1944) in Miles and Grigson (1990), Dahlberg (1945, 1947, 1968), Robinson (1956), Le Gros Clark (1960), Swindler (1976, personal communication 1995), Wood and Abbott (1983), Wood et al. (1983,

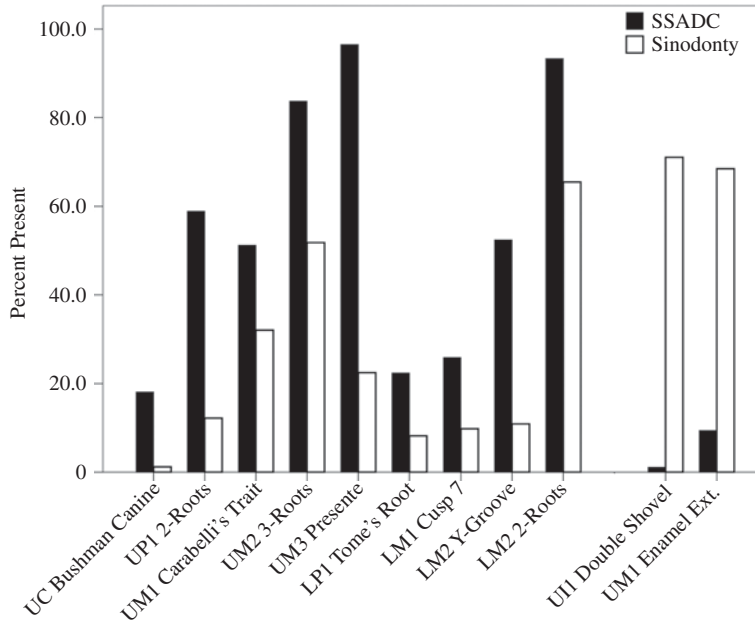

Figure 12.2. Bar graph illustrating differences in percentages of traits constituting the SSADC in pooled samples of (1) sub-Saharan Africans (Irish 1997) and (2) Northeast Asian/New World Sinodonts (Turner 1985). See text for details.

1988), Hillson (1986), Wood and Engleman (1988), Aiello and Dean (1990), Tobias (1991), Turner and Hawkey (1991), Turner (1992b), Brown and Walker (1993), Stringer (personal communication, 1997), and Irish (personal observations). More recently, Irish and Guatelli-Steinberg (2003) noted that the Bushman canine is an apparent exception, though it was found in Neanderthals (Irish 1998a; Stringer et al. 1997).

Zubov (1992a, b) described two additional sub-Saharan high-frequency traits that are found in hominins, including australopithecines, *Homo habilis*, *Homo erectus*, and early *Homo sapiens*. The first is the type 1 upper incisor of Mizoguchi (1985), a form of shoveling where weak marginal lingual ridges converge toward the tooth cervix; it differs from the forms of shoveling expression observed in Neanderthals and modern humans (e.g., Sinodonts). The second trait, the LM1 epicristid of Hershkovits (1971), is expressed as a middle trigonid crest between the protoconid and metaconid (Liu Wu and Turner 1993). Zubov (1992a:6) concluded that "the presence of such traits suggests retention of local ancestral features [in sub-Saharan Africans] since very remote times." Other nonmetric traits not in the SSADC but common in sub-Saharan Africans, including UI1 labial curvature, UI1 midline diastema

Table 12.1. *Dental trait percentages (%) and number of individuals (n) for the original pooled sample SSADC [(n = 966 dentitions), on which the Sub-Saharan African Dental Complex was based], the Current pooled sub-Saharan sample (n = 2512) discussed in the chapter, and six sub-samples of the latter derived according to age and geographic region, respectively*

SAMPLE		SSADC	*Current*	*Ancient*	*Recent*	*Western*	*Central*	*Eastern*	*Southern*
TRAITS									
High Frequency									
Bushman canine UC	%	*18.1*	20.6	20.3	20.6	17.5	15.1	11.2	27.1
(+ = ASU 1–3)	n	*586*	1351	227	1124	246	159	286	660
Root no. UP1	%	*58.9*	60.5	53.7	62.1	59.2	62.6	67	55.1
(+ = ASU 2+)	n	*570*	1345	257	1088	321	179	388	457
Carabelli's trait UM1	%	*51.2*	51.3	39.7	53.1	55.6	54.6	56.6	45.7
(+ = ASU 2–7)	n	*683*	1705	232	1473	302	196	435	772
Root no. UM2	%	*83.7*	78.5	68.9	81.5	80.4	79	80.3	75.4
(+ = ASU 3+)	n	*503*	1076	251	825	271	143	304	358
UM3 Presence	%	*96.5*	95.2	97.2	94.7	96.5	97.2	95	94.1
(+ = ASU +)	n	*708*	2027	422	1605	423	246	561	797
Tome's root LP1	%	*22.4*	17.1	17.4	17	26	20.5	17.2	11.3
(+ = ASU 3–5)	n	*361*	1112	253	859	250	127	273	462
Cusp 7 LM1	%	*25.9*	28	19	30.4	24.8	23.4	24.9	31.2
(+ = ASU 2–4)	n	*598*	1619	343	1276	294	154	353	818
Groove pattern LM2	%	*52.4*	63.3	67	62.2	55.7	72.6	67.6	62.2
(+ = ASU Y)	n	*617*	1652	373	1279	296	175	370	811
Root no. LM2	%	*93.3*	91.7	86.4	93.5	94.1	91.8	90.2	91.1
(+ = ASU 2)	n	*388*	978	250	728	254	97	245	382
Low frequency									
Double shovel UI1	%	*1.1*	1	0.9	1	2.2	0	1.2	0.8
(+ = ASU 2–6)	n	*437*	1018	234	784	137	100	168	613
Enamel extension UM1	%	*9.4*	4.8	7.6	4.2	13.9	2	2.1	1.9
(+ = ASU 1–3)	n	*574*	1637	288	1349	381	200	437	619
Other high frequency									
UI1 labial curvature	%	*55.5*	56.8	52.5	58.1	52.1	50.5	46.6	62
(+ = ASU 2–4)	n	*425*	1028	236	792	144	107	174	603
UI1 midline diastema	%	*12.7*	10.5	10	10.6	10.8	15	8.2	10.6
(+ = > 0.5mm)	n	*709*	1810	270	1540	325	187	437	861

Note: Ancient (n = 489) and Recent (n = 2023), plus Western (n = 486), Central (n = 325), Eastern (n =637), and Southern (n = 1064) sub-Saharan Africa. See text for sample details.
Sources: The ASUDAS breakpoints under each trait are from Irish (1993, 1997) and Scott and Turner (1997).

(discussed later), and upper and lower molar hypocones and hypoconulids, are also present in fossil specimens. All told, it appears that traits that best characterize sub-Saharan Africans (particularly those in the SSADC) are "ancestral" in origin – which prompted me to suggest that of all living populations, those

from south of the Sahara Desert may be the least derived dentally from the common ancestor of anatomically modern humans (Irish 1997, 1998a).

The first attempt to quantify such a possibility involved an MMD comparison of traits in the pooled sub-Saharan African and six world samples (mentioned in Introduction) with those in three hominin samples: (1) Krapina Neanderthals and published data from (2) gracile and (3) robust australopithecines (Irish 1998a). All hominins showed the closest dental affinity to sub-Saharan Africans on the basis of similar occurrences of ancestral traits; of the three, the gracile australopithecines were especially close. Moreover, MMD distances increased between the hominins and remaining modern samples with greater geographic distance from sub-Saharan Africa; the frequencies of all ancestral traits decreased accordingly.

A second, more comprehensive attempt (Irish and Guatelli-Steinberg 2003) to quantify the ancestral state of trait expression in the SSADC involved comparison of the same pooled sub-Saharan Africans, the 13 samples in Figure 12.1, and data directly recorded in the dental remains of (1) *Paranthropus* (*P. robustus, P. boisei*); (2) *Australopithecus* (*A. africanus, A. anamensis, A. afarensis, A.* indet.); and (3) *Homo* (*H. habilis, H. rudolfensis, H. ergaster/erectus*, and *H.* indet). For statistical purposes (MMD and PCA noted previously), these African specimens were pooled into two samples: "robust" (i.e., *Paranthropus*) and "gracile" (all others); the latter was assumed to represent species that are most likely ancestral to modern humans.

A two-dimensional PCA plot of intersample variation from Irish and Guatelli-Steinberg (2003) (not shown) is essentially identical to that in Figure 12.1. The main difference is inclusion of the robust and gracile hominins, which, compared to all modern samples, were again closest to sub-Saharan Africans. With respect to the x-axis (Component 1), the hominins were plotted at the far left; the first component accounts for more than 50 percent of the more than 80 percent variance explained by the plot. As mentioned, parallel results were obtained using other quantitative methods, including two-dimensional multidimensional scaling (Kruskal and Wish 1978) of the intersample MMD distances.

Intersample patterning results from the same factors in both the previously published (Irish and Guatelli-Steinberg 2003) and current PCA plots (Figure 12.1). Although other traits contribute, it is evident that much variation is related to those in the SSADC, based on PCA loadings in Component 1 (not shown). Specifically, other than Bushman canine – which is important on Component 2 – strong negative loadings for high-frequency SSADC traits heavily influenced sample location on the x-axis. These, among others, are ancestral traits common in early hominins and modern Africans. Samples toward the right on the x-axis (e.g., Sinodonts) are characterized by derived traits with strong positive loadings – including high

frequencies of UI1 double shoveling and UM1 enamel extension. Therefore, these frequencies seemingly identify an expansive west-to-east/ancestral-to-derived dental cline that runs from sub-Saharan Africa, into North Africa, Europe, Southeast and Northeast Asia, and the New World. This finding provides additional, independent evidence for an "Out-of-Africa" movement of early humans (Irish 1998a; Irish and Guatelli-Steinberg 2003; also see Hanihara, this volume).

12.4 Updated sub-Saharan African dental trait frequencies

The preceding findings are promising in that the 11 SSADC traits helped "locate" sub-Saharan peoples. However, the Sub-Saharan African Dental Complex was based on pooling 17 spatially disparate samples of 966 individuals that are largely synchronic. It was, therefore, intended as a preliminary characterization. Thanks to National Science Foundation funding of the author for a project on the "Bantu Expansion" (see Beleza et al. 2005; Cavalli-Sforza et al. 1996; Ehret 1982, 2000; Fage 1995; Greenberg 1966; Hiernaux 1975; July 1992; Nurse et al. 1985; Phillipson 2005, for historical background), the numbers of sub-Saharan samples (n = 52) and individuals (n = 2,512) were markedly increased (Figure 12.3). Because coverage of the subcontinent improved, it is now possible to assess potential regional trends. These totals now include 11 samples of 489 individuals dating from the Late Paleolithic through Iron Age, which facilitate diachronic study. Thus, the objective is to refine the dental characterization of sub-Saharan Africans and, in the process, reassess and augment the SSADC.

In Figure 12.4 only minor fluctuations in trait presence exist between the original and newly pooled sub-Saharan samples. Some changes are more obvious than others, including an increase in the high-frequency LM2 Y-groove pattern and decrease in the low-frequency UM1 enamel extension traits that serve to strengthen their inclusion in the SSADC. Yet the overall pattern remains constant. Relative to the 13 other samples in Figure 12.1, only three-rooted UM2 and LP1 Tome's root declined enough to question their African specificity: 83.7 to 78.5 percent ($\chi^2 = 5.75$, df = 1, $p < 0.05$) and 22.4 to 17.1 percent ($\chi^2 = 5.21$, df = 1, $p < 0.05$), respectively (Table 12.1). A comparison with the other world samples (see tables in Lipschultz 1996; Scott and Turner 1997; Irish and Guatelli-Steinberg 2003) reveals that the new UM2 three-root trait percent is now on par with that of North Africans (78.6 percent), and less than that of Australians (80.9 percent) and West Asians (88.2 percent); the latter figure, however, may not be representative of regional variation given its derivation from a small sample of mostly Natufians (Lipschultz 1996). The original Tome's root value was second only

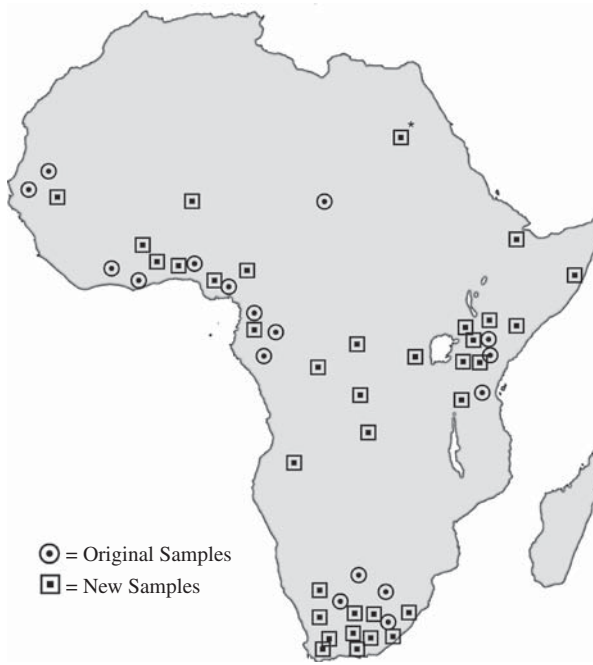

Figure 12.3. Origin locations of the 17 original and 35 new individual samples that were pooled to make the "global" sub-Saharan African sample. See text for details.

* Sample derived from the Late Paleolithic site of Jebel Sahaba, which was demonstrated to comprise dentitions exhibiting sub-Saharan dental trait frequencies (Irish 1993, 1997).

to that of the Australians (27.3 percent); the new one is now also less than that of Southeast Asians (21.9 percent), and analogous to the occurrence in South Siberians (17.3 percent) and Micronesians (17.5 percent).

The pattern of trait occurrences illustrated by the bar graph in Figure 12.5 (and Table 12.1) is quite similar between pooled "recent" (2,023 individuals) and "ancient" (489 individuals) samples. The main difference is that the ancient sample has slightly lower occurrences of high-frequency UC Bushman canine, two-rooted UP1, UM1 Carabelli's trait, three-rooted UM2 (which contributes to the decrease between original and new samples), LM1 cusp 7, and two-rooted LM2; of these, three differ significantly ($\chi^2 > 3.84$, df = 1, $p < 0.05$): UM1 Carabelli's, UM2 three-roots, and LM1 cusp 7. The ancient dentitions also exhibit more enamel extensions. This variation is driven by slightly lower complexity in the dentitions of early Kenyans and Tanzanians (n = 175) and, to a lesser extent, South Africans (n = 207). The reason for less complexity or,

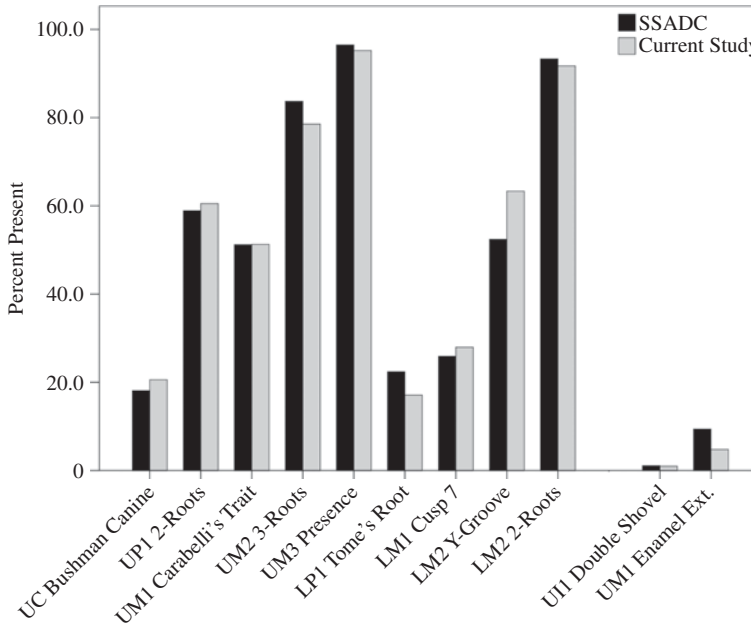

Figure 12.4. Bar graph illustrating percentages of trait presence in (1) the original 17 sub-Saharan samples used to derive the SSADC (Irish 1997) and (2) all 52 samples combined for the current study. See text for details.

conversely, more mass-additive traits in the recent sample is probably related to the aforementioned Bantu Expansion. In brief, between 4,000 and 3,000 BP agriculturalist proto-Bantu peoples began to expand south and east from their homeland in Nigeria and Cameroon (July 1992; Newman 1995; Ruhlen 1994; Vogel 1997). In some cases, migration(s) continued into the mid-nineteenth century AD (Fage 1995; July 1992). These dentally complex western Africans (see later discussion) moved across the subcontinent replacing indigenous groups (e.g., Holocene eastern and southern Africans) and/or contributing to the latter's gene pools. Today, ancestors of these western emigrants account for a majority of Africa's peoples and are colloquially termed "Bantu" – after the linguistic term used to classify a group of more than four hundred related languages (Ehret 2000; Greenberg 1966; Heine and Nurse 2000; Williamson and Blench 2000).

Finally, there is overall trait consistency across sub-Saharan Africa. In Figure 12.6 and Table 12.1 the subcontinent is divided into western, central, eastern, and southern regions. Intraregion diversity is, of course, documented (not shown), as is common in morphological and genetic markers:

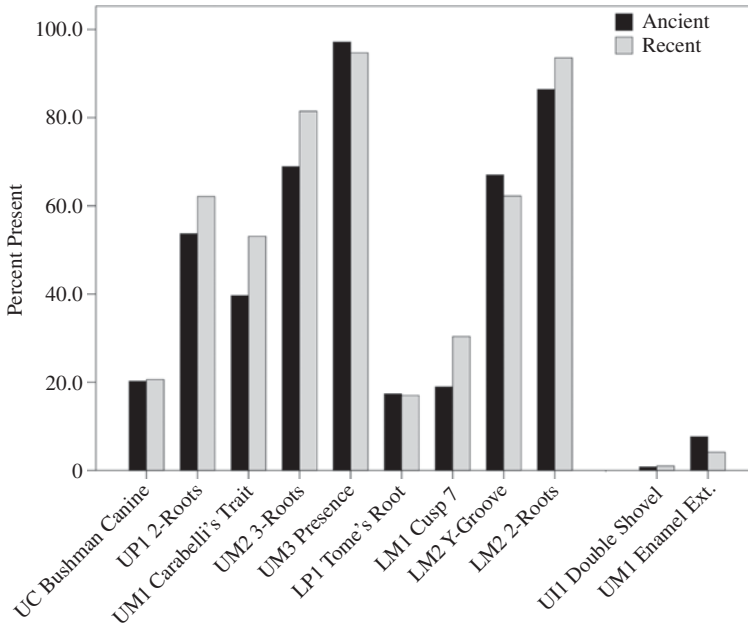

Figure 12.5. Bar graph illustrating percentages of trait presence in pooled samples composed of 1) "recent" (n = 2,023) and 2) "ancient" (n = 489) sub-Saharan individuals. See text for details.

for example, LP1 Tome's root varies from 0 percent to 36 percent among 11 eastern African samples. Interregion variation is illustrated; for example, the western Africans have higher UM1 enamel extension, among other complex traits. Southern Africans appear different for several traits – though in a uniform fashion. That is, it can be seen that they differ from eastern Africans for two-rooted UP1 ($\chi^2 > 3.84$, df = 1, $p < 0.05$). One likely reason for the difference is the presence of many Khoisan and early Holocene individuals in the southern sample; the same explanation accounts for the high percentage of Bushman canine, as the trait name implies, as well as the lower numbers of LP1 Tome's and other root traits. Although "African" in all respects, Khoisan (i.e., San and Khoikhoi) have many unique features relative to other sub-Saharan groups, including Bantu – with which less admixture occurred than might be expected; much of this information is detailed by Tobias (1972, 1974), among others (Excoffier et al. 1987; Hiernaux 1975; Tishkoff et al. 2009). This uniqueness also applies to their teeth, which express many mass-additive traits on small crowns anchored by relatively small, simple roots (Haeussler et al. 1989; Irish 1993).

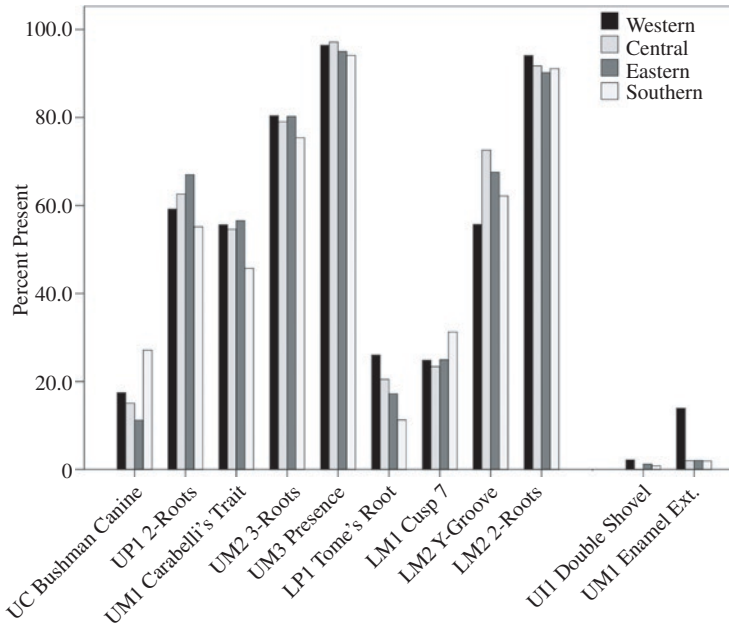

Figure 12.6. Bar graph illustrating percentages of trait presence in (1) western, (2) central, (3) eastern, and (4) southern regional pooled sub-Saharan African samples. See text for details.

12.5 The Afridont dental pattern

Despite some trait variation among pooled sub-Saharan samples comprising (1) original and new, (2) ancient and recent, and (3) four geographic regions, an overall pattern of uniformity is clearly evident (Table 12.1 and Figures 12.4–12.6). The original versus new is particularly alliterative, with some observed variation attributable to the larger numbers of ancient eastern and southern Africans. The three-rooted UM2 and Tome's root numbers decreased, but they still rank among the highest globally. In any event, individual traits are not overly important in and of themselves; several are "found in comparable frequencies in other world samples, but [it is] the appropriate combination of all traits [that] clearly identifies a [s]ub-Saharan pattern" (Irish 1998a: 87). Moreover, if only recent population samples were characterized, that is, if ancient (pre-Bantu) data were excluded, the original and new sub-Saharan samples would be more or less identical. Nonetheless, in accordance with the SSADC as originally defined, all aboriginal sub-Saharan African peoples collectively share similar percentages of the 11 traits. On this basis, it has largely withstood the test of time and additional, corroborative data.

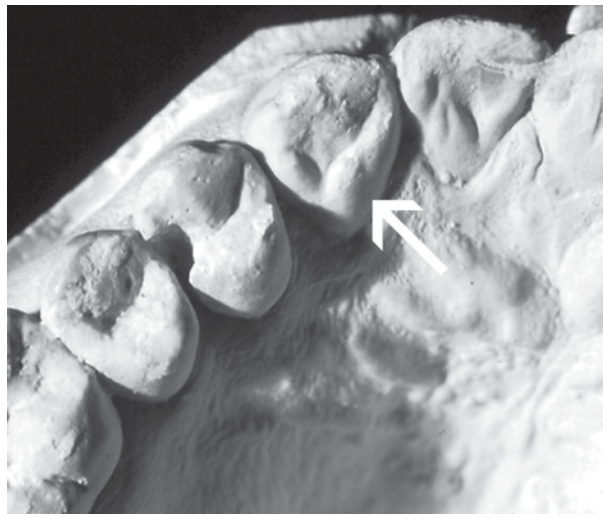

Figure 12.7. Arrow points to large UC mesiolingual ridge incorporating a tuberculum dentale that, together, form a grade 3 Bushman canine according to ASUDAS standards.

To reiterate, those high-frequency traits that best characterize the greater sub-Saharan African population since the Pleistocene and across the subcontinent are Bushman canine, two-rooted UP1, UM1 Carabelli's trait, three-rooted UM2, LM2 Y-groove, LM1 cusp 7, LP1 Tome's root, two-rooted LM2, and UM3 presence. In addition, these diverse peoples share among the lowest frequencies of UI1 double shoveling and UM1 enamel extension. The specific ASUDAS breakpoints used to determine "presence" are listed under each trait in Table 12.1; the rationale for each is presented in Irish (1993, 1998b) and Scott and Turner (1997). All traits are described in detail and illustrated to some extent in other sources (Irish 1993, 1998b; Scott and Turner 1997; Turner et al. 1991). Of these, UC Bushman canine (Figure 12.7) and, to a lesser extent, LM1 cusp 7 (Figure 12.8) are clearly the "most" African of all, given their rarity outside the continent. In addition, sub-Saharan Africans appear to express relatively high frequencies of UI1 labial curvature (Figure 12.9) and UI1 midline diastema (Figure 12.10). Unfortunately, these traits are not routinely recorded in other populations. Yet, as mentioned, both are found in extinct and extant hominoids and early hominins – including those species mentioned earlier (personal observation by author). The former trait is part of the ASUDAS; the latter is defined in Irish (1993, 1998b).

Non-SSADC traits aside, I conclude this chapter by recommending, after the analysis of 35 additional African samples relative to many others defined

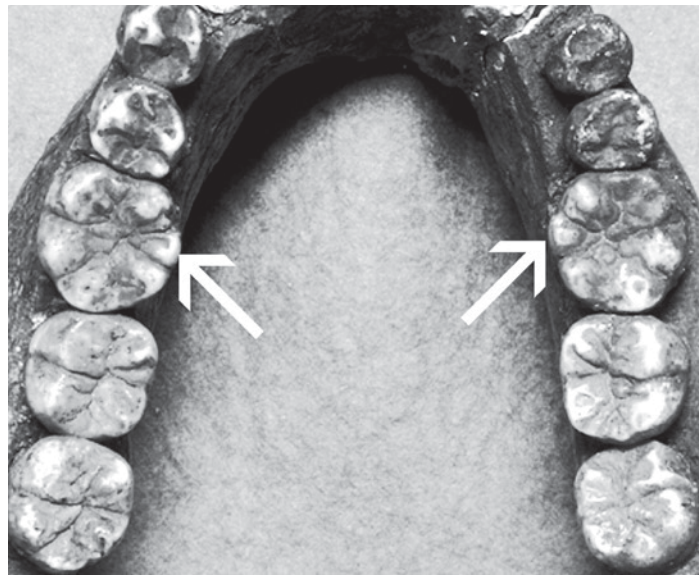

Figure 12.8. Arrows point to bilaterally expressed cusp 7 trait on left and right LM1s. On the basis of ASUDAS standards both are recordable at grade 4.

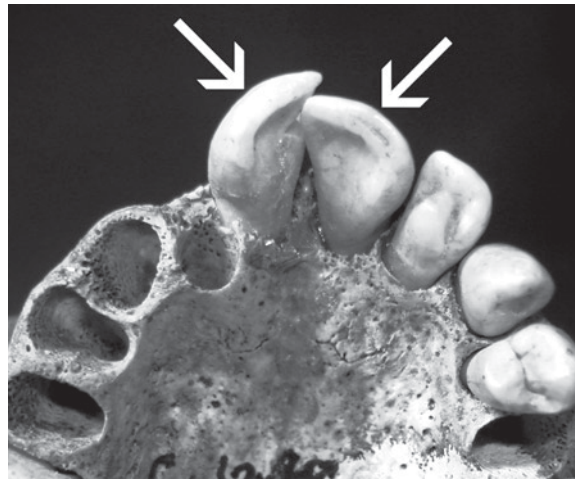

Figure 12.9. Arrows point to ASUDAS grade 4 labial curvature expression on right and left UI1s.

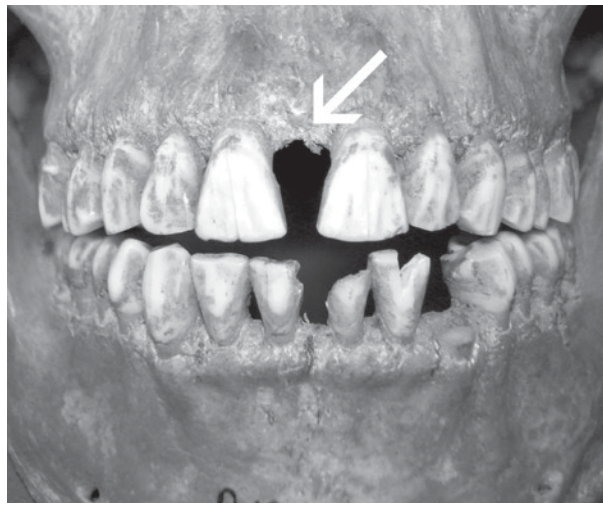

Figure 12.10. Arrow indicates large UI1 midline diastema. See text for details.

at a global level (Lipschultz 1996; Scott and Turner 1997), that use of the preliminary SSADC label be discontinued. The validity of this suite of traits has been confirmed by the new data. Therefore, following standard dental morphological nomenclature, including Sinodont, Sundadont (Turner 1985, 1987), Indodont (Hawkey 1998, 2004), and Eurodont (Scott and Dorio 2010), I propose that the more definitive term "Afridont" be employed to characterize the sub-Saharan population dentally. Beyond broad categorization, Afridonty can be used for, among other objectives, a better understanding of human origins, assisting in the estimation of biological affinity at local, regional, and global levels, and potential forensic identification of individuals.

Acknowledgments

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13 *Basque dental morphology and the "Eurodont" dental pattern*

G. RICHARD SCOTT, ALBERTO ANTA, ROMAN SCHOMBERG, AND CONCEPCION DE LA RÚA

13.1 Introduction

The Basque peoples of northern Spain and southern France have long held the interest of anthropologists and linguists. Linguistically, they are considered an isolate with no close ties to any surrounding Indo-European-speaking group. This linguistic peculiarity raised expectations that a similar situation would be found at the biological level. In the early twentieth century, studies of Basque cranial morphology were mostly typological in nature, as researchers made every effort to identify a distinctive Basque type (MacClancy 1993; de la Rúa et al. 2005/2006 for a review). In the 1930s, the discovery of remains at the site of Urtiaga (Gipuzkoa), which presumably dated to the Upper Paleolithic, pushed the origins of the Basque population further back in time. This led to a popular hypothesis that the "Basque type" reflected an indigenous and local evolution of the Cro-Magnon race (Aranzadi and Barandiaran 1948). Later radiometric dating of these skulls unequivocally placed the Urtiaga remains in the more recent Bronze Age, a finding that challenged the Cro-Magnon hypothesis of Basque origins (Altuna and de la Rúa 1989).

In the mid-twentieth century, blood antigen typing replaced cranial typology in addressing questions of population origins. Cumulative information on more than a single locus seemed to confirm the idea that Basques were a locally evolved population that had descended from Upper Paleolithic Europeans. Seemingly, Basques survived the impact of genetic admixture with later migrants (Near East Neolithic farmers) to a greater extent than other European populations

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(Calafell and Bertranpetit 1994a, b; Cavalli-Sforza 1988; Bertranpetit and Cavalli-Sforza 1991; Mourant 1947).

Research on a broad array of "classic genetic polymorphisms" (blood groups, serum proteins, and enzymes) pointed to the idea that the genetic distinctions of the Basque population had not been completely erased despite substantial gene flow from neighboring populations (Calafell and Bertranpetit 1994a). In a detailed synthesis of worldwide genetic data in *The History and Geography of Human Genes,* Cavalli-Sforza et al. (1994) analyzed European gene frequency variation and found Indo-European-speaking populations clustered closely with one another. The most notable European outliers were Sardinians and three non-Indo-European groups – Lapps, Finns, and Basques. Synthetic maps also suggested the Basques were distinct, especially the map based on the fifth principal component of European gene frequencies (Cavalli-Sforza et al. 1994:294). Some authors, however, contend that the methodology employed for multiple genetic data analyses (mainly synthetic maps derived from principal components analysis) may lead to spurious results (Sokal et al. 1991).

While there are numerous publications on the genetics of Basque populations, the metrics of skeletal remains have received much less attention. In contrast to the earlier typological studies of Basque skulls in the 1930s and 1940s, recent studies adopt a statistically driven craniometric approach to the issue of Basque origins and relationships (cf. de la Rúa 1992; Janzen 2011; Lalueza Fox et al. 1996). Assessing Basque cranial morphology, de la Rúa (1992) concluded that complex morphometric and multivariate analyses revealed some differentiation of Basques from Iberic populations.

Recent debate has focused on ascertaining whether Basques are the best representative population of Paleolithic Europe. Some authors contend that demic diffusion during the Neolithic had a profound impact on the genetic profile of modern Europeans (Ammerman and Cavalli-Sforza 1984; Barbujani et al. 1994, 1995; Bellwood 2001). Others suggest the genetic impact of Neolithic farmers on Europeans is evident but is not as pronounced as the demic diffusion model suggests (Richards 2003; Zvelebil 1998, 2000). A recent study on the mtDNA diversity of hunter-gatherers and first farmers in northern Spain proposed a random dispersion model for Neolithic farmers in Europe, contradicting the total acculturation and replacement models developed to explain Neolithization (Hervella et al. 2012).

Recently, genetic studies of Basque populations have focused on DNA polymorphisms, including mtDNA and nuclear markers on both autosomal and sex chromosomes (Alonso et al. 2005; Bertranpetit et al. 1995; Brion et al. 2003; Izagirre and de la Rúa 2001; Izagirre et al. 2001). The extensive literature on Basque genetics focuses on several themes (Alonso 2008): (1) internal relationships, or population structure; (2) external relationships, to neighboring or

distant groups; and (3) distinctive or unique markers in the Basque population that suggest the ancestry of Basques can be traced back to pre-Neolithic populations in Western Europe.

The isolation of Basques has resulted in some genetic heterogeneity among Basque subpopulations with respect to non-Basques in Y-chromosome but not in mtDNA lineages (Martínez-Cruz et al. 2012). These discordant results in paternal and maternal lineages explain, at least partially, the contradictory findings that support (Alfonso-Sanchez et al. 2008; Calderon et al. 2000; Iriondo et al. 2003; Manzano et al. 1996, 2002) and reject (Comas et al. 1998; Rodriguez-Ezpeleta et al. 2010) genetic heterogeneity in Basques. Still, some intrinsic level of genetic structure is present among Basque populations that may be a consequence of different cultural, geographic, and historic factors.

Regarding the relationship of Basques to other European populations, recent data on uniparental Y-chromosome lineages indicate Basques are similar to other Western European populations, although they show slight frequency differences. It has been suggested that some other Western European populations might exhibit the genetic distinctiveness of the populations inhabiting the Basque region, but that this peculiarity is not linked to having a Basque culture (language) (Martínez-Cruz et al. 2012). Finally, on the topic of distinctive or unique genetic markers in the Basque population, several lines of evidence indicate at least some (DNA) lineages (alleles) have evolved *in situ*, probably since pre-Neolithic times (Alonso and Armour 1998). This supports the idea that the ancestry of Basques can be traced back to pre-Neolithic populations in Western Europe.

Given the widespread interest in the question of Basque origins, it is not surprising there are dozens of publications on genetic and cranial diversity. Surprisingly, we know almost nothing about the Basque dentition. Worldwide surveys of tooth crown size (Kieser 1991) and dental morphology (Scott and Turner 1997) make no mention of Basque dental variation. Our aim is to use an entirely new set of biological characteristics to determine whether Basques from northern Spain exhibit a unique dental morphological profile, that is, one that distinguishes them from Indo-Europeans to the north and east, and Afro-Asiatic neighbors to the south.

13.2 Materials and methods

Morphological observations were made on living Basques, Spanish, and mixed Basque/Spanish individuals, as well as historic remains from the Cathedral of Santa Maria, Vitoria (Alava province); the latter date from the eleventh to nineteenth centuries. In 2005, crown traits were scored on 145 dental casts (36 Basque, 61 Spanish, 48 Basque-Spanish) collected by Alberto Anta at the Dental

department of the University of the Basque Country (UPV/EHU). Although data were collected in Bilbao, individuals could have come from any of the Basque provinces. In 2006 and 2008, crown and root traits were scored on 460 skeletons disinterred from the Cathedral of Santa Maria, Vitoria, Spain, under the direction of Agustin Azkarate Garai-Olaun and his associates; burial records are not exact, but it is estimated that more than 75 percent of the individuals were of Basque heritage. Vitoria attracted merchants and travelers from other countries so there are non-Basque elements in the sample, but these would be in a decided minority (Jaione Agirre-Garcia, personal communication). Although we can provide an initial characterization of Basque tooth crown and root morphology, we are not in a position to address such issues as Basque population structure. Dental variation among Basque subpopulations in Spain and France is likely, but this issue will have to be addressed when more regional samples have been studied.

Following the Arizona State University Dental Anthropology System (ASUDAS; Turner et al. 1991), 16 crown traits were scored on 29 teeth for presence and degree of expression in each dental cast. Two crown traits (Bushman canine, enamel extensions) were not scored on casts but were recorded for skulls. Eighteen crown traits, six root traits, and missing/pegged/reduced UM3 were scored on teeth of the historic remains. As crown and root traits are not sexually dimorphic, data for males and females were combined (Scott and Turner 1997). Regarding issues of left and right sides, the individual count method was followed whereby an individual was classified according to the antimere that exhibited the greatest degree of trait expression (Scott 1980).

Crown frequencies for the four samples from northern Spain were compared to 25 worldwide composite groups from Scott and Turner (1997). Given the limitation of casts, analysis involved nine crown traits: UI1 shoveling, three-cusped UM2, UM1 Carabelli's trait, four-cusped LM1 and LM2, Y-groove pattern on LM2, and cusp 6, cusp 7, and the deflecting wrinkle on LM1. To include root traits and focus specifically on Western Eurasian populations, 15 traits (11 crown, four root) were compared between the historic Vitoria sample and 16 geographic groups from Europe, North Africa, the Middle East, and India. Distance values were derived through Nei's genetic distance program in NTSYS; cluster analysis of these intersample values based on UPGMA and the neighbor-joining method yielded congruent trees; as such, only the UPGMA results are shown.

13.3 Results

In compiling comparative data on Western Eurasian and other world groups, a recurrent hindrance is the use of different traits and breakpoints.

Table 13.1. *Total crown and root trait frequencies for key teeth by breakpoint*

Trait	Tooth	Breakpoint	Spanish	Living Spanish-Basque	Basque	Cathedral of Santa Maria	Compared to World
Winging	UI1	1–3/0–3	0.017	0.000	0.000	0.096	Low
Shoveling	UI1	3–6/0–7	0.034	0.043	0.083	0.044	Low
Double shoveling	UI1	2–6/0–6	0.017	0.021	0.000	0.030	Low
Tuberculum dentale	UI2	2–6/0–6	0.258	0.392	0.200	0.226	Low
Interruption grooves	UI2	1/0–1	0.196	0.044	0.200	0.295	Intermediate
Bushman canine	UC	1–3/0–3				0.022	Low
Distal accessory ridge	LC	1–5/0–5	0.281	0.282	0.229	0.130	Low
Multiple lingual cusps	LP2	2–7/0–7	0.557	0.673	0.778	0.514	High
3-Cusped (-hypocone)	UM2	0–1/0–5	0.184	0.303	0.285	0.320	High
Carabelli's cusp	UM1	5–7/0–7	0.033	0.063	0.112	0.209	High
Carabelli's cusp	UM1	2–7/0–7	0.567	0.624	0.778	0.659	High
Cusp 5	UM1	1–5/0–5	0.228	0.244	0.193	0.225	Low
Enamel extensions	UM1	2–3/0–3				0.032	Low
Pegged/missing	UM3	1/0–1				0.116	Intermediate
4-Cusped (-hypoconulid)	LM1	0/0–5	0.086	0.174	0.114	0.076	High
4-Cusped	LM2	0/0–5	0.850	0.933	0.886	0.868	High
Y-Pattern	LM2	Y/Y-X-+	0.220	0.235	0.190	0.148	Low
Cusp 6	LM1	1–5/0–5	0.125	0.178	0.182	0.079	Low
Cusp 7	LM1	2–4/0–4	0.036	0.088	0.086	0.070	Low
Protostylid	LM1	2–7/0–7	0.018	0.023	0.000	0.000	Low
Deflecting wrinkle	LM1	3/0–3	0.128	0.174	0.435	0.202	Low
2-Rooted	UP1	2-rooted/total				0.516	Intermediate
3-Rooted	UM2	3-rooted/total				0.609	Intermediate
2-Rooted	LC	2-rooted/total				0.092	High
Tome's root	LP1	4–7/0–7				0.138	Low
3-Rooted	LM1	3-rooted/total				0.013	Low
1-Rooted	LM2	2-rooted/total				0.763	Intermediate

Source: Defined in Scott and Turner (1997).

For that reason, full trait frequency distributions are presented in the Appendix for 18 crown traits (31 teeth), six root traits (six teeth), and pegged/missing/reduced UM3 for the Spanish, Basque, Spanish-Basque, and historic samples. The focus in the analysis and discussion is on trait frequencies for key teeth using the most common breakpoints (Scott and Turner 1997).

13.3.1 Characterization of Basque tooth crown and root morphology

Data for 18 crown traits, six root traits, and UM3 agenesis for the four samples from northern Spain are presented in Table 13.1. In the far right column, the

array of frequencies are noted as low, intermediate, or high relative to other world populations (Scott and Turner 1997).

Europeans are more often characterized by the absence or rarity of traits rather than by their presence (Mayhall et al. 1982; Lee and Scott 2011); Basques are no exception to this generalization. Traits that are absent or relatively infrequent in the Spanish/Basque samples include UI1 winging, shoveling, and double shoveling and UI2 *tuberculum dentale*, UC Bushman canine, LC distal accessory ridge, UM1 cusp 5 and enamel extensions, LM2 Y-groove pattern, and LM1 cusp 6, cusp 7, protostylid, and deflecting wrinkle. Tome's roots of LP1 and three-rooted lower first molars are also rare or in low frequency. Five traits show intermediate frequencies: UI2 interruption grooves, UM3 agenesis, two-rooted UP1, three-rooted UM2, and two-rooted LM2. Five traits found in high frequencies relative to other world populations include LP2 multiple lingual cusps, UM1 Carabelli's cusp, three-cusped UM2, and four-cusped LM1 and LM2. For roots, the most distinctive variant is the two-rooted lower canine; the Basque frequency is high even by European standards (Alexandersen 1962, 1963; Lee and Scott 2011). For high frequency traits, two involve crown simplification (hypocone loss on UM2 and hypoconulid loss on LM1 and LM2) rather than elaboration.

13.3.2 Distance analysis: Basques versus world samples based on nine crown traits

Phenetic distances, computed between the four samples from northern Spain and 25 world populations (composite samples in Scott and Turner 1997), serve as the basis for the UPGMA cluster diagram in Figure 13.1. Three fundamental divisions are evident in the dendrogram: the deepest break is for sub-Saharan Africans, followed by a division between Asian/Pacific populations on one hand, and Western Eurasians on the other. Focusing on Basques, the historic sample is the most highly differentiated group within the Western Eurasian cluster. Remarkably, there is no single variable among the nine crown traits that sets the historic Basque sample apart. The differences are minor yet act in concert to separate the Santa Maria sample from all remaining groups in the cluster. The next sample to split off is the living Basque and, in this case, an unusually high frequency of deflecting wrinkle may contribute to the result. The Basque and Spanish-Basque samples cluster closely together, as part of the third split in this grouping. All remaining Western Eurasian populations are tightly clustered. Compared to African and Asian/Pacific populations, Western Eurasians are the most coherent and least differentiated group from a dental morphological standpoint.

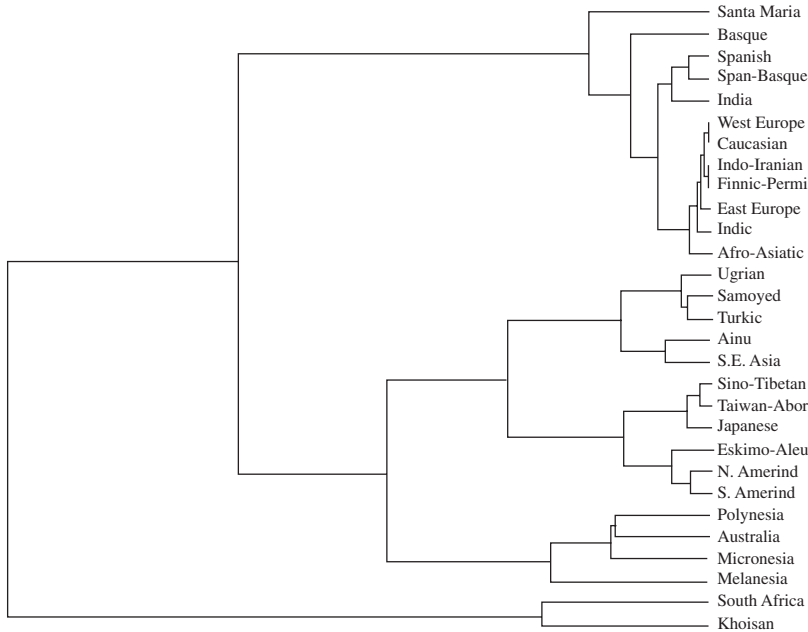

Figure 13.1. UPGMA dendrogram showing relationship of historic and modern Basques to world populations.

13.3.3 Basques compared to Western Eurasian populations

Table 13.2 presents data for 11 crown and four root traits in 16 samples from Europe, North Africa, the Middle East, and South Asia. The mean trait frequency, standard deviation, and coefficient of variation for each trait are listed at the bottom of the table, along with frequencies for living Basques and the historic sample from Santa Maria.

Dental trait frequency variation among Western Eurasian groups has two primary sources: (1) between group differentiation brought about by founder effect/genetic drift during colonization events that occurred mostly during the Holocene, and (2) sampling error. Prior to the wide adoption of the ASUDAS, a third source of variation would be inter-observer error. This error is much less of a problem than it was before 1980. Data in the table were obtained mostly by researchers trained at Arizona State University and/or who used ASUDAS standards (Turner et al. 1991).

Overall, dental variation among Western Eurasians is minor, corroborating results from the first analysis. Linguistically, groups in the sample are mostly

Indo-European and Afro-Asiatic. The two exceptions, in addition to Basques, are Finland (Finnic-Permian, Uralic language family) and early South Asia, where language attribution is problematic (Elamo-Dravidian?). The Finnish sample shows the highest frequency of shoveling, the lowest frequency of 2-rooted UP1, and no 2-rooted lower canines – all of which align them with North Asian populations. However, no other trait stands out in a Western Eurasian context; this pattern is also evident for Finns in genetic markers of the blood (Nei and Roychoudhury 1988). Early South Asia but not Late South Asia is distinctive for the absence of 2-rooted canines, low frequency of 2-rooted UP1, high frequency of UM1 cusp 5, high frequency of 3-rooted UM2, and high frequency of LM1 cusp 6. These five traits fall in the direction of Southeast Asian dental variation, yet the remaining nine traits are more consistent with Western Eurasia. The issue cannot be resolved here, but these data suggest a residual effect from aboriginal Indian populations who were biologically allied with Southeast Asians, compounded by late Holocene invasions from the Middle East (see Hemphill, this volume).

The two Basque samples at the bottom of Table 13.2 share more similarities with Western Eurasians than either the Finns or early South Asians. UI2 *tuberculum dentale* is at the low end of the frequency range while 2-rooted lower canines are at the high end viz. Western Eurasians. For the most part, however, Basques do not exhibit any trait that sets them apart from neighboring Indo-European or Afro-Asiatic populations in North Africa and the Levant.

13.3.4 Distance analysis of Western Eurasian populations based on dental traits

The dendrogram based on a distance analysis of 15 traits among 17 Western Eurasian groups is shown in Figure 13.2. Two groups stand out while the others fail to reveal natural geographic groupings. Finland, with several traits aligning it with North Asia, breaks out first as the most highly differentiated group in the dendrogram. Finns are followed by early South Asians with a number of frequencies that align them with Southeast Asia rather than Western Eurasia. The historic Basque sample does not separate out from the cluster as shown in Figure 13.2; it instead clusters with England and the Levant. Northwest Africa clusters with the Nile Valley, as expected, but they also group with Denmark, a finding less expected. Overall, this analysis shows that Basques are not distinct enough from other Western Eurasian groups to indicate they are a clear-cut outlier.

Table 13.2. *Basque crown and root trait variation in the context of Western Eurasian populations*

Trait:	SHOV	T.D.	Root#	MLC	Root#	HYP	C5	EnExt	Root#	C Abs	4-Cusp	Y Gr	C6	C7	Root#
Tooth:	UI1	UI2	LC	LP2	UP1	UM2	UM1	UM1	UM2	UM3	LM2	LM2	LM1	LM1	LM2
Italy (1)	0.074	0.538	0.027	0.561	0.527	0.195	0.196	0.090	0.712	0.114	0.829	0.238	0.018	0.061	0.850
NW Africa (2)	0.106	0.339	0.057	0.689	0.523	0.326	0.104	0.035	0.758	0.184	0.675	0.395	0.116	0.061	0.895
Nile Valley (3)	0.262	0.407	0.018	0.696	0.631	0.162	0.141	0.193	0.722	0.127	0.750	0.271	0.103	0.025	0.830
Denmark (4)	0.053	0.256	0.057	0.596	0.576	0.145	0.429	0.017	0.654	0.086	0.884	0.274	0.162	0.089	0.859
England (4)	0.028	0.255	0.053	0.593	0.310	0.274	0.101	0.008	0.597	0.114	0.731	0.208	0.092	0.038	0.767
Holland (4)	0.000	0.405	0.083	0.537	0.361	0.333	0.125	0.030	0.460	0.172	0.892	0.205	0.040	0.063	0.659
Ireland (4)	0.111	0.667	0.033	0.790	0.386	0.109	0.186	0.038	0.603	0.106	0.711	0.287	0.067	0.034	0.659
Scotland (4)	0.068	0.301	0.112	0.653	0.394	0.179	0.309	0.072	0.711	0.085	0.718	0.232	0.167	0.048	0.785
Greenland (5)	0.000	0.455	0.092	0.603	0.363	0.182	0.340	0.035	0.636	0.125	0.766	0.342	0.233	0.065	0.750
Norway (5)	0.000	0.535	0.043	0.457	0.600	0.241	0.204	0.011	0.641	0.160	0.910	0.194	0.105	0.032	0.762
Finland (6)	0.437	0.437	0.000	0.469	0.083	0.208	0.125	0.139	0.500	0.145	0.791	0.220	0.091	0.084	0.767
Levant (7)	0.075	0.160	0.040	0.785	0.480	0.245	0.050	0.019	0.935		0.925	0.265	0.015	0.030	1.000
Mallorca (8)		0.193		0.725		0.324	0.283				0.739	0.142	0.050	0.000	
France (9)		0.667	0.016	0.619	0.450	0.195	0.225				0.847				
Early SA (10)	0.128	0.280	0.000	0.581	0.139	0.312	0.361	0.042	0.905	0.154	0.704	0.300	0.376	0.051	0.833
Later SA (10)	0.112	0.384	0.037	0.457	0.430	0.268	0.105	0.129	0.528	0.210	0.815	0.330	0.099	0.110	0.876
Mean	**0.104**	**0.392**	**0.045**	**0.613**	**0.417**	**0.231**	**0.205**	**0.061**	**0.669**	**0.137**	**0.793**	**0.260**	**0.116**	**0.053**	**0.804**
S.D.	0.1178	0.1536	0.0324	0.1057	0.1561	0.0700	0.1103	0.0564	0.1372	0.0379	0.0806	0.0651	0.0926	0.0281	0.0890
C.V.	1.13	0.39	0.72	0.17	0.37	0.30	0.54	0.92	0.21	0.27	0.10	0.25	0.80	0.53	0.10
Basque (L)	0.083	0.200		0.777		0.286	0.228				0.886	0.190	0.182	0.036	
Basque (SM)	0.044	0.258	0.092	0.513	0.516	0.320	0.224	0.032	0.609	0.116	0.868	0.148	0.079	0.070	0.763

Sources: (1) Coppa et al., 1998, 2007; Vargiu et al., 2009; (2) Irish, 2000; (3) Irish, 1993; (4) Adler, 2005; (5) Scott and Alexandersen, 1992; (6) Salo, 2005; (7) Ullinger et al., 2005; (8) Garcia Savoli, 2009; (9) Laforest et al., 2011; (10) Hawkey, 2002.

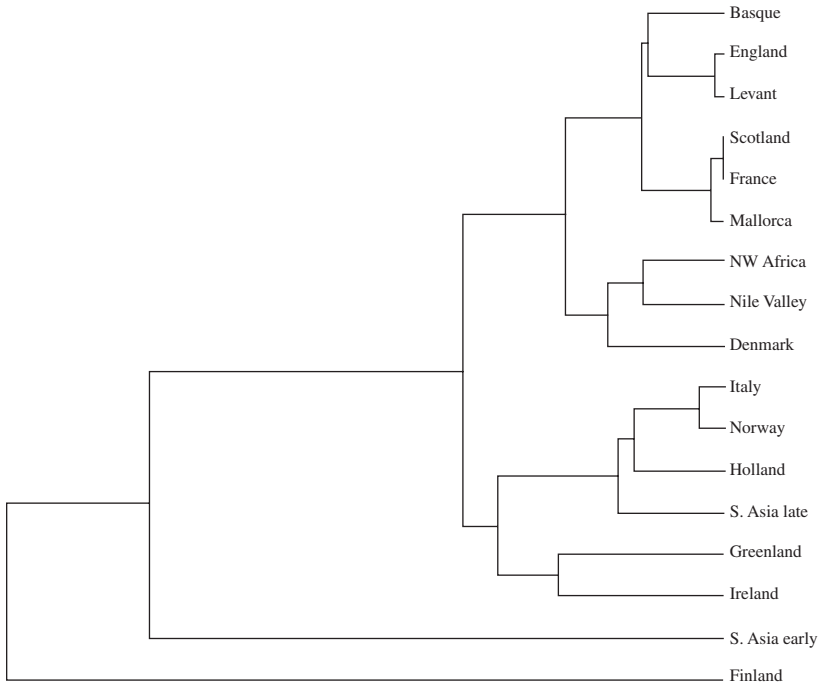

Figure 13.2. UPGMA dendrogram showing relationship of historic Basque sample from Cathedral of Santa Maria (Vitoria, Spain) to Western Eurasian populations.

13.4 Discussion

Although Basques show a general Western Eurasian dentition, the first cluster analysis indicates they are somewhat distinct in the context of world populations, yet still align with Europeans. This result parallels findings from genetics that Basques fall within the European sphere but as something of an outlier. Using gene frequency data from Roychoudhury and Nei (1988), we analyzed European samples for 12 serum protein and red cell enzyme systems (14 alleles) and eight blood group systems (nine alleles). The number of European samples for any given system ranged from 13 to 36, with most falling in the twenties. We calculated a European mean, the 95 percent confidence limits, and range for each allele. Although Basque gene frequencies usually fall within the range of Europeans, they fell outside the 95 percent confidence limit for 19 of 23 alleles. In seven of twenty-three cases, the Basque frequency was outside the range of European frequencies. This finding was especially marked for properdin factor B, where allele BF S was markedly lower (0.562) than the European

mean (0.773); conversely, allele BF F11 was considerably higher in Basques (0.145) relative to the European mean (0.014). A single Portuguese sample precluded Basques from being outside the range of Europeans for RH*r, but they were well above the 95 percent confidence limits for the allele that has long set Basques apart from other Europeans. ABO*B also falls outside the range of all other Europeans, with the exceptionally low frequency of 0.032 (viz. range of 0.044–0.222).

For crown and root traits, Basques show a similar pattern when analyzed in the context of Western Eurasians. For extant Basques, seven of nine crown trait frequencies fall outside the 95 percent confidence limits of Western Eurasian samples. For the historic sample, eight of fifteen traits are outside the Western Eurasian 95 percent confidence limits. UI2 *tuberculum dentale* and LM2 Y-groove pattern are less frequent in the Basques, while two-rooted lower canines, two-rooted UP1, and four-cusped LM2 are notably higher in one or both samples. As with genetic markers, Basques show dental differences from European, North African, and Middle Eastern groups, but there is no single feature that sets them apart.

13.4.1 "Caucasoid" dental complex

On the basis of the analysis of American white dental cast collections, Mayhall et al. (1982) defined the "Caucasoid dental complex of the permanent dentition," which included (1) absent or trace shoveling; (2) no bilateral winging; (3) no premolar occlusal tubercles, or odontomes; (3) Carabelli's trait often expressed as a cusp or bulge; (4) LM1 protostylid rare or absent; (5) LM1 cusp 6 rare or absent; and (6) cusp 7 rare or absent. They reported three-cusped UM2 frequencies of about 30 percent, but they did not include this trait in the dental complex.

Our analysis of Basque dental morphology, along with numerous other studies on European, Middle Eastern, North African, and Indian populations undertaken in the past 50 years (Adler 2005; Aksianova 1979; Aksianova et al. 1977, 1979; Alexandersen 1962, 1963; Bailey 2006; Brabant and Ketelbant 1975; Coppa et al. 1998, 2007; Cucina et al. 1999; Desideri and Besse 2010; Du Souich 2002; Gadzhiev 1979; García Savoli 2009; Gauta et al. 2010; Guatelli-Steinberg et al. 2001; Hawkey 1998, 2002; Irish 1993, 2000, 2006; Ismagulov and Sikhimbaeva 1989; Johnson and Lovell 1994; Kaczmarek 1992; Kaul and Prakash 1981; Khaldeeva 1979; Kirveskari 1974; Kochiev 1979; Laforest et al. 2011; Lipschultz 1997; Lukacs 1987; Pilloud 2009; Roler 1992; Rosenzweig and Zilberman 1967, 1969; Salo 2005; Scott and Alexandersen 1992; Senyurek 1952; Sofaer et al. 1986; Ullinger et al. 2005; Vargiu et al. 2009; Weets 2004;

Figure 13.3. Characteristic "Eurodont" traits: (A) Carabelli's cusp on UM1 so large that is shows exposed dentine, (B) typical spatulate and mostly featureless upper incisors, (C) two-rooted lower canine, (E) five-cusped LM1 and four-cusped LM2. (Please see color plate section.)

Zubov 1968), extends the Caucasoid dental complex to include a number of additional traits. In keeping with Turner's dental distinction between North (Sinodonts) and Southeast (Sundadonts) Asians and Irish's designation of an Afridont pattern for sub-Saharan Africans (this volume), we propose "Eurodont" as a shorthand term for Western Eurasian dental morphological variation. Characteristic crown and root expression includes:

1. Low frequency traits (traits uncommon/infrequent in Western Eurasians): UI1 winging, UI1 shoveling, UI1 double shoveling; Bushman canine; UM1 enamel extensions; LM2 Y pattern; LM1 cusp 6; LM1 cusp 7; LM1 protostylid; LM1 deflecting wrinkle; three-rooted lower first molars.
2. High frequency traits (traits most common in Western Eurasians): high frequency of UM1 Carabelli's cusp/tubercle forms; two or more lingual cusps LP2; three-cusped UM2; four-cusped LM1 and LM2; two-rooted lower canines (Figure 13.3).

13.4.2 Primitive and derived

As a follow-up to extensive studies of dental morphological variation in recent African populations, Irish (1998; Irish and Guatteli-Steinberg 2003) extended

observations to the hominin fossil record to evaluate the degree to which various geographic populations exhibited primitive or derived dentitions. On the basis of a large number of trait comparisons, he found sub-Saharan Africans showed the fewest derived traits of all world populations, in accord with the recent "out of Africa" model for the origins of anatomically modern humans.

To determine how primitive or derived the Basque dentition is on a world scale, we adopted an approach that does not require comparisons to earlier hominin fossils. On the basis of monomorphic characteristics of hominoid and early fossil hominin dentitions, we utilized eleven traits that were either 0 percent or 100 percent in the ancestral population. Twelve world populations and the Basques were then compared to this standard. Traits assumed to be 0 percent in the ancestral condition include three-cusped UM2, premolar odontomes, two-rooted lower canines, four-cusped LM1, four-cusped LM2, three-rooted LM1, and pegged/missing/reduced UM3. Traits assumed to be 100 percent include two-rooted UP1, three-rooted UM2, two-rooted LM2, and Y-pattern LM2.

When trait frequencies of regional groups were compared to "ancestral standards" to estimate relative distance, a distinct pattern emerged. First, the least derived world populations are sub-Saharan Africans (0.058) and Bushmen (0.073) – a finding in accord with Irish (1998; Irish and Guatelli-Steinberg 2003). Groups from Southeast Asia and the Pacific exhibit a uniform and intermediate level of derived traits: Southeast Asia Early (0.137), Australia (0.140), Polynesia (0.155), Melanesia (0.157), and Southeast Asia Late (0.163). Groups that exhibit the most derived dentitions in the world are about equally distant from the presumed ancestral condition but for entirely different reasons. Primarily on the basis of root number reduction, the distance values for North Asian and derivative populations are American Indian (0.287), China-Mongolia (0.310), and Eskimo-Aleut (0.373). Distance values for Western Eurasians are very similar to North Asian/New World values (i.e., Western Europe [0.287], Basque [0.359]), but this finding is attributable to crown simplification (e.g., hypocone and hypoconulid reduction) rather than root reduction. Western Eurasians in general and Basques in particular have dentitions that are highly derived from the standpoint of tooth crown and root morphology.

13.5 Conclusions

Observations of tooth morphology in living Basque and Spanish populations show the former differs slightly from the latter, as well as from other

modern Europeans. This finding may be a function of conservative dental morphological differentiation through time or gene flow with neighboring non-Basque populations. More likely, it is a combination of the two processes. The Basque dentition shows the typical Eurodont dental pattern of minimal incisor shoveling, doubleshoveling, and winging, and a moderate frequency of UI2 interruption grooves. Lower molars are characterized by relatively high frequencies of four-cusped LM1 and LM2 and low frequencies of LM1 cusps 6 and 7. The deflecting wrinkle frequency is unusually high in the living Basque sample, but this may be a function of small sample size.

Cavalli-Sforza and other geneticists have adopted the view that the present day populations of Europe were strongly influenced by actual migrations of farming populations from Anatolia; however, many archaeologists take issue with this conclusion. Zvelebil (1998, 2000; Zvelebil and Zvelebil 1988) contends there is no archaeological evidence to support a major migration into Europe at the onset of the Neolithic. Richards (2003:157) notes that "Near Eastern farmers played their part, but the majority of European genetic lineages have their roots in the European Palaeolithic." Recent research suggests that modern European mitochondrial DNA diversity had a predominantly Paleolithic origin, with a Neolithic contribution of 23 percent (Richard et al. 1996; Richard 2003). Although Basques do not exhibit a heretofore unrecognized dental morphological pattern, the possibility that they are living descendants of late Paleolithic populations in Western Europe is not precluded. However, on the basis of their similarities to other Western Eurasian populations, they may not be alone in that regard.

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Appendix 13.1. *Crown and root traits for living Basque, Spanish, Basque-Spanish, and medieval/postmedieval skeletons from the Cathedral of Santa Maria, Vitoria, Spain*

				Grade							
Trait	Tooth	Sample	n	0	1	2	3	4	5	6	7
Winging	UI1	Spanish	60	98.3	1.7						
		Basque	35	100.0	0.0						
		Spanish-Basque	47	100.0	0.0						
		Santa Maria	136	90.4	5.9	2.2	1.5				
Shoveling	UI1	Spanish	59	37.3	45.8	13.6	3.4	0.0	0.0	0.0	0.0
		Basque	36	19.4	55.6	16.7	8.3	0.0	0.0	0.0	0.0
		Spanish-Basque	46	39.1	37.0	19.6	4.3	0.0	0.0	0.0	0.0
		Santa Maria	135	67.4	20.0	8.1	4.4	0.0	0.0	0.0	0.0
	UI2	Spanish	60	41.7	43.3	13.3	1.7	0.0	0.0	0.0	0.0
		Basque	36	27.8	52.8	13.9	5.6	0.0	0.0	0.0	0.0
		Spanish-Basque	46	43.5	41.3	15.2	0.0	0.0	0.0	0.0	0.0
		Santa Maria	128	56.3	30.5	9.4	3.9	0.0	0.0	0.0	0.0
Double-shoveling	UI1	Spanish	60	93.3	5.0	1.7	0.0				
		Basque	35	100.0	0.0	0.0	0.0				
		Spanish-Basque	47	93.6	4.3	2.1	0.0				
		Santa Maria	133	97.0	1.5	0.8	0.8				
Interruption grooves	UI1	Spanish	58	100.0	0.0						
		Basque	35	97.1	2.9						
		Spanish-Basque	45	100.0	0.0						
		Santa Maria	149	95.3	4.7						
	UI2	Spanish	56	80.4	19.6						
		Basque	35	80.0	20.0						
		Spanish-Basque	45	95.6	4.4						
		Santa Maria	139	70.5	29.5						
Tuberculum dentale	UI1	Spanish	58	24.1	44.8	22.4	8.6				
		Basque	36	22.2	38.9	27.8	11.1				
		Spanish-Basque	45	37.8	28.9	26.7	6.7				
		Santa Maria	134	62.7	14.9	13.4	9.6				
	UI2	Spanish	59	41.4	32.8	17.2	6.9	1.7	0.0		
		Basque	35	20.0	60.0	8.6	11.4	0.0	0.0		
		Spanish-Basque	46	28.3	32.6	28.3	10.9	0.0	0.0		
		Santa Maria	129	54.3	24.8	13.2	4.7	3.1	1.6		
	UC	Spanish	61	39.3	23.0	23.0	13.1	1.6	0.0		
		Basque	34	29.4	38.2	11.8	17.6	2.9	0.0		
		Spanish-Basque	46	41.3	23.9	23.9	10.9	0.0	0.0		
		Santa Maria	118	61.0	18.6	13.6	2.5	4.2	3.4		
Distal accessory ridge	UC	Spanish	55	16.4	30.9	29.1	20.0	1.8	1.8		
		Basque	35	28.6	25.7	28.6	17.1	0.0	0.0		
		Spanish-Basque	47	25.5	10.6	44.7	14.9	2.1	2.1		
		Santa Maria	82	56.1	3.7	11.0	25.6	3.7	0.0		

Appendix 13.1. (*cont.*)

Trait	Tooth	Sample	n	Grade 0	1	2	3	4	5	6	7
	LC	Spanish	57	71.9	22.8	3.5	1.8	0.0	0.0		
		Basque	35	77.1	20.0	2.9	0.0	0.0	0.0		
		Spanish-Basque	39	71.8	23.1	5.1	0.0	0.0	0.0		
		Santa Maria	153	86.9	3.9	5.2	3.9	0.0	0.0		
Bushmen canine	UC	Santa Maria	92	97.8	2.2	0.0					
Root number	LC	Santa Maria	295		91.5	8.8	0.4				
Multiple lingual cusps	LP1	Spanish	56	64.3	8.9	1.8	14.3	8.9	1.8		
		Basque	35	60.0	11.4	5.7	11.4	8.6	2.9		
		Spanish-Basque	48	52.1	12.5	10.4	14.6	6.3	4.2		
		Santa Maria	226	88.9	0.9	7.5	0.9	0.0	1.3		
	LP2	Spanish	61	37.8	6.6	21.3	19.7	4.9	9.8		
		Basque	35	19.4	2.8	33.3	25.0	13.9	5.6		
		Spanish-Basque	46	23.9	8.7	21.7	21.7	10.9	13.0		
		Santa Maria	181	48.1	0.6	22.1	16.0	10.5	2.8		
Root number	UP1	Santa Maria	169		48.4	51.6					
Tome's root	LP1	Santa Maria	234	60.7	4.0	13.8	7.6	9.8	4.0		
Hypocone	UM1	Spanish	60	0.0	1.7	0.0	0.0	61.7	36.7		
		Basque	36	0.0	0.0	0.0	11.1	61.1	27.8		
		Spanish-Basque	47	0.0	0.0	0.0	0.0	59.6	40.4		
		Santa Maria	235	0.4	0.4	0.0	3.4	34.5	61.7		
	UM2	Spanish	60	11.7	6.7	3.3	43.3	35.0	0.0		
		Basque	35	11.4	17.1	5.7	54.3	11.4	0.0		
		Spanish-Basque	43	7.0	23.3	0.0	48.8	20.9	0.0		
		Santa Maria	200	26.5	5.5	3.0	42.5	21.5	1.0		
	UM3	Santa Maria	100	66.0	9.0	9.0	12.0	4.0	0.0		
Carabelli's trait	UM1	Spanish	60	25.0	18.3	21.7	20.0	11.7	0.0	3.3	0.0
		Basque	36	13.9	8.3	25.0	25.0	16.7	2.8	5.6	2.8
		Spanish-Basque	48	18.8	18.8	27.1	14.6	14.6	2.1	2.1	2.1
		Santa Maria	144	28.5	5.6	9.7	16.0	19.4	12.5	6.3	2.1
Cusp 5	UM1	Spanish	57	77.2	17.5	5.3	0.0	0.0			
		Basque	31	80.6	16.1	0.0	3.2	0.0			
		Spanish-Basque	41	75.6	19.5	4.9	0.0	0.0			
		Santa Maria	138	77.5	9.4	11.6	0.7	0.7			
Enamel extensions	UM1	Santa Maria	156	96.8	1.3	1.9					
Root number	UM2	Santa Maria	169		17.2	21.9	60.9				
Pegged/ missing/red	UM3	Santa Maria	86	88.4	11.6						

(*continued*)

Appendix 13.1. (*cont.*)

				Grade							
Trait	Tooth	Sample	n	0	1	2	3	4	5	6	7
Cusp number	LM1	Spanish	58	8.6	0.0	8.6	24.1	50.0	8.6		
		Basque	35	11.4	0.0	2.9	40.0	40.0	5.7		
		Spanish-Basque	46	17.4	0.0	10.9	39.1	30.4	2.2		
		Santa Maria	198	7.6	0.5	1.5	17.7	42.9	29.8		
	LM2	Spanish	60	85.0	6.7	5.0	3.3	0.0	0.0		
		Basque	35	88.6	2.9	5.7	2.9	0.0	0.0		
		Spanish-Basque	45	93.3	2.2	2.2	0.0	2.2	0.0		
		Santa Maria	189	86.8	2.1	4.2	6.3	0.5	0.0		
	LM3	Santa Maria	112	56.3	6.3	1.8	8.0	13.4	14.3		
Groove pattern	LM1	Spanish	30		96.7	0.0	3.3				
		Basque	19		89.5	0.0	10.5				
		Spanish-Basque	24		79.2	0.0	20.8				
		Santa Maria	186		90.3	8.6	1.1				
	LM2	Spanish	41		22.0	7.3	70.7				
		Basque	21		19.0	0.0	81.0				
		Spanish-Basque	34		23.5	2.9	73.5				
		Santa Maria	149		14.8	4.0	81.2				
	LM3	Santa Maria	76		14.5	2.6	81.6				
Cusp 6	LM1	Spanish	56	87.5	12.5	0.0	0.0	0.0	0.0		
		Basque	33	81.8	9.1	9.1	0.0	0.0	0.0		
		Spanish-Basque	45	82.2	11.1	6.7	0.0	0.0	0.0		
		Santa Maria	139	92.1	2.9	5.0	0.0	0.0	0.0		
Cusp 7	LM1	Spanish	57	80.7	15.8	1.8	1.8	0.0	0.0		
		Basque	35	77.1	14.3	5.7	2.9	0.0	0.0		
		Spanish-Basque	45	75.6	15.6	2.2	2.2	4.4	0.0		
		Santa Maria	185	93.0	0.0	2.7	2.7	0.5	1.1		
Protostylid	LM1	Spanish	57	98.2	0.0	1.8	0.0	0.0	0.0		
		Basque	34	100.0	0.0	0.0	0.0	0.0	0.0		
		Spanish-Basque	44	97.7	0.0	2.3	0.0	0.0	0.0		
		Santa Maria	147	100.0	0.0	0.0	0.0	0.0	0.0		
	LM2	Spanish	60	96.7	1.7	1.7	0.0	0.0	0.0		
		Basque	35	97.1	0.0	2.9	0.0	0.0	0.0		
		Spanish-Basque	44	97.7	0.0	0.0	0.0	0.0	2.3		
		Santa Maria	99	96.0	0.0	0.0	3.0	0.0	1.0		
Deflecting wrinkle	LM1	Spanish	39	87.2	12.8						
		Basque	23	56.5	43.5						
		Spanish-Basque	23	82.6	17.4						
		Santa Maria	89	79.8	20.2						
3RM1	LM1	Santa Maria	152	98.7	1.3						
Root number	LM2	Santa Maria	198		23.7	76.3					

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14 *A first look at the dental morphometrics of early Palauans*

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14.1 Introduction

The settlement of Remote Oceania, the last large area of the globe to be occupied by humans, occurred within the last 5,000 years and appears to correlate with the spread of the Austronesian language family. Possibly originating in Taiwan, coastally adapted Austronesians spread southward through the Philippines, New Guinea, and the Bismarck Archipelago, to culminate in the Lapita expansion into the Pacific (Bellwood 1997, 2004; Spriggs 1999, 2007). Although this migration is well-documented after the appearance of the Lapita culture in the Bismarck Islands ca. 3,300 years ago (Kirch 1987, 2000; Summerhayes 2007), the routes and timing of Austronesian movement during the previous 1,700 years are relatively unknown.

Because it is the westernmost island group of Micronesia, equidistant (750 km) from the Philippines, Halmahera in the Moluccas, and New Guinea, Palau is in a unique location to record the dispersal of pre-Lapita peoples. Three lines of evidence indicate that Palau was first inhabited during earlier stages of the southward Austronesian march: (1) paleoenvironmental data derived from cores that record swamp taro (*Cyrtosperma chamissonis*) pollen suggest occupation before 4000 BP (Athens and Ward 2001; Wickler 2001); (2) calibrated radiocarbon dates show residence in the islands was established by at least 3200 BP (Anderson et al. 2005; Clark 2004, 2005; Liston 2005); and (3) the Palauan language, a member of the Western Malayo-Polynesian suborder (Pawley and Ross 1993; Tryon 1995) or stand-alone primary subgroup of the Malayo-Polynesian branch (Donohue and Denham 2010) of Austronesian, has earlier origins than the Oceanic branch of Polynesia; this finding may indicate Palau was settled before the Oceanic split from Malayo-Polynesian.

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With regard to this evidence, we focus on human remains recovered from the cemetery at Chelechol ra Orrak, in the Republic of Palau. Dating to ca. 3000 BP (Fitzpatrick 2003) and representing at least twenty-five individuals, the cemetery is one of the earliest and largest of its kind in Remote Oceania (Nelson and Fitzpatrick 2006). It was excavated in three stages by Fitzpatrick (in 2000 and 2007) and Fitzpatrick and Nelson (2002). The skeletal assemblage comprises prenates, neonates, adolescents, and adults of both sexes (Nelson and Fitzpatrick 2006). Although many skeletal elements are fragmentary, several nearly complete, articulated, and well-preserved individuals have been recorded, though not all have been recovered. Included in the recovered material are four nearly complete crania with whole or partial dentitions and many isolated teeth. Currently, the small sample of elements limits the data that can be collected and the scope with which they can be used to assess biological affinities. However, teeth make up a preponderance of the elements and constitute a reasonable sample size; thus, a morphometric analysis was undertaken to estimate the relationship of these early Palau inhabitants to other populations in the region.

Morphological traits of tooth crowns and roots are under strong genetic control (Scott and Turner 1997), and the study of morphological variation across populations has been a valuable tool in deciphering genetic and evolutionary relationships among various human populations (Turner 1976, 1983a; Hanihara 1992; Irish 1998, 2006; Irish and Guatelli-Steinberg 2003). Most pertinent to this study is the research by Turner (1983b, 1987, 1990a), who delineated the Sinodont/Sundadont dichotomy in patterns of dental morphological variation in Asia and the western Pacific. Although some dental traits have been recorded in prehistoric samples from Guam (Leigh 1929; Turner 1990b; Douglas et al. 1997; Hanihara 1998), few samples from other areas within Micronesia have been analyzed to determine whether they fall within the Sinodont and Sundadont groups. In cases where dental morphology has been analyzed, Micronesia is often treated as a single entity because of consistently small sample sizes in specific island groups (Turner 1990b; Scott and Turner 1997). Here we examine the dental morphology of the early inhabitants of Palau to determine (1) their affinities to other Micronesians and (2) where they fit within the Sinodont/Sundadont division.

Like morphology, tooth size appears to be strongly heritable (Goose 1971; Townsend and Brown 1978). Dental metrics are often considered less robust than morphology in differentiating among samples because (1) environmental conditions during fetal development appear to affect tooth size (Garn et al. 1979; Kieser 1992; Kieser and Groeneveld 1998) and (2) the amount of dental reduction varies among populations depending on myriad factors (Brace et al. 1991; Calcagno 1989; Calcagno and Gibson 1991). However, in a large cross-cultural,

Table 14.1. *The eight dental morphology traits used in this analysis with range of expression and breakpoint at which expression is deemed significant or is scored (e.g., four-cusped LM2)*

Trait	Range of Expression	Breakpoint
UI1 Shoveling	0–6 (none – marked shoveling)	3–6 (semishovel to marked)
UI1 Double shoveling	0–6 (none – extreme)	2–6 (trace to extreme)
UP1 Root number	1, 2, or 3 (roots)	1 root
UM1 Enamel extension	0–3 (none – >4 mm)	2–3 (medium ca. 2 mm and large >4 mm)
UM3 Peg/reduced/agenic	Presence/absence	Presence
LM1 Deflecting wrinkle	0–3 (absent-large L-shaped)	2–3 (ridge deflected but no contact with cusp 4 and ridge is L-shaped and contacts cusp 4)
LM1 Root number	1, 2, or 3 (roots)	3 roots
LM2 Cusp number	4, 5, or 6 (cusps)	4 cusps

Sources: Turner 1990a; Turner et al. 1991.

multivariate study, Harris and Rathbun (1991) found that variation in tooth size does show differences among populations. For this study, tooth size comparisons are used as another means of judging where the Orrak sample falls in terms of phenotypic variation within the western Pacific and Asia.

14.2 Materials and methods

The dental and gnathic sample from Orrak comprises four maxillae and three mandibles associated with adult crania, several fragmentary maxillae and mandibles, and 112 isolated permanent teeth. Dental morphology was scored by the first author using the Arizona State University Dental Anthropology System (ASUDAS) (Scott and Turner 1997; Turner et al. 1991). Sexes were pooled following the standard protocol for dental morphological studies (Hanihara 1992; Irish 1997). However, instead of using the individual count method (Irish 2006; Turner and Scott 1977), all teeth were included in the analysis; though not preferable, this approach was necessary given the large number of isolated teeth and corresponding problems in identifying individuals. For this study, the Orrak sample was compared to data compiled by Turner using the eight traits (Table 14.1) he deems most useful in separating Sinodonts from Sundadonts (Turner 1990a, b). Comparisons utilized occurrence rates of the various traits as either present/absent or at the breakpoints defined by Turner (1990a; see Table 14.1).

Buccolingual and mesiodistal crown diameters (Hillson 1996; Wolpoff 1971) of the 227 available teeth were recorded by the first author using a Mitutoyo

Table 14.2. *Mesiodistal and buccolingual tooth diameters of the Orrak dental sample*

	Mesiodistal			Buccolingual		
Tooth	N	Mean	s.d.	N	Mean	s.d.
UI1	12	9.36	0.640	11	7.58	0.557
UI2	16	7.44	0.393	16	7.05	0.395
UC	21	8.35	0.467	21	8.47	0.581
UP1	15	7.34	0.555	15	10.16	0.435
UP2	17	7.34	0.351	17	10.07	0.346
UM1	20	11.26	0.741	20	11.93	0.667
UM2	15	10.51	0.790	15	11.73	1.004
UM3	14	9.48	1.277	14	11.44	1.286
LI1	14	5.50	0.304	14	6.30	0.236
LI2	11	6.42	0.231	11	6.57	0.465
LC	9	7.32	0.309	9	7.81	0.419
LP1	15	7.55	0.410	14	8.71	0.342
LP2	11	7.90	0.515	11	9.21	0.443
LM1	17	12.22	0.914	17	11.42	0.647
LM2	14	11.76	0.620	14	11.21	0.728
LM3	6	12.31	0.469	6	11.14	0.523

digital caliper calibrated to .01 mm (Table 14.2). Because approximately 50 percent of the teeth were isolated finds, metric analysis is by tooth class only, with sexes pooled; again, this approach is not ideal but is used out of necessity. Dental metric data from Orrak were compared with samples from East and Southeast Asia, Australia, and Near and Remote Oceania (Table 14.3). Mean mesiodistal and buccolingual diameters and tooth crown areas were analyzed in their raw state across all teeth, as well as for the anterior, postcanine, and M1-M2 subsets. Principal components analysis was used to explore which teeth and/or dimensions were most important in discriminating among groups; discriminant analysis was employed to examine group relatedness. Scatterplots of the raw values were created to illustrate the position of Orrak within the continuum of tooth size relative to the comparative samples.

14.3 Results

14.3.1 Dental morphology

Comparing Orrak trait frequencies with those compiled for samples from East Asia, Mainland and Insular Southeast Asia, Near and Remote Oceania, and

Table 14.3. *Samples used in comparative dental metrics analysis*

Series	N*	Time Period	Location	Source
China				
Chinese (20)	46	Recent	Manchuria	Hanihara 1998
Anyang (21)	21	Bronze Age	Henan Prov.	Matsumura 1994
Chifeng (22)	38	Late Bronze-Iron Age	Inner Mongolia	Matsumura 1994
Northern Chinese (23)	149	Recent	N. China	Matsumura 1994
Weidun (24)	56	Neolithic	Changzhou, Jiangsu	Yamaguchi and Xianghong 1995
Japan				
Ainu (25)	8–61		Hokkaido	Hanihara 1998
Jomon, Hokaido (26)	20–77	Neolithic	Hokkaido	Hanihara 1998
Jomon (27)	711	Neolithic	All Japan	Matsumura 1994
Recent Japan (28)	47–50	Recent	Honshu	Hanihara 1998
Yayoi 1 (29)	212	Aeneolithic	Kyushu	Matsumura 1994
Yayoi 2 (30)	60	Aeneolithic	Tanegashima	Matsumura 1994
Mainland Southeast Asia				
Mainland SE Asia (31)	10–19	Recent	Malay Pen.	Hanihara 1998
Early Thailand (32)	15–27	Early Metal Age	Thailand	Hanihara 1998
Neolithic Thailand (33)	58	Neolithic		Matsumura 1994
Modern Thailand (34)	110	Recent	Bangkok	Matsumura 1994
Early Laos (35)	12	Early Holocene	Laos	Matsumura and Hudson 2005
Modern Laos (36)	57	Recent	Laos	Matsumura and Hudson 2005
Guar Kepah (37)	27	Mid. Holocene	Malaysia	Matsumura and Hudson 2005
Ban Kao (38)	37	Mid. Holocene	Thailand	Matsumura and Hudson 2005
Non Nok Tha (39)	15	Mid. Holocene	Thailand	Matsumura and Hudson 2005
Insular Southeast Asia				
Negrito 1 (40)	19–23	Recent	Luzon	Hanihara 1998
Negrito 2 (41)	37	Recent	Luzon	Matsumura and Hudson 2005
Negrito 3 (42)	–	Recent		Kanazawa et al. 2000
Indonesia (43)	47	Recent	Pan Indonesia	Matsumura 1995
Andaman Is. (44)	69	Recent	Andaman Is.	Matsumura and Hudson 2005
Dayak 1 (45)	7–11	Recent	Borneo	Hanihara 1998
Dayak 2 (46)	74	Recent	Borneo	Matsumura and Hudson 2005
Sumatra (47)	41	Recent		Matsumura and Hudson 2005
Lesser Sunda (48)	20	Recent	Sulawesi, Timor, Java	Matsumura and Hudson 2005

(*continued*)

Table 14.3. (*cont.*)

Series	N*	Time Period	Location	Source
Filipino 1 (49)	10–27	Recent	Philippines	Hanihara 1998
Filipino 2 (50)				
Filipino 3 (51)	–	Recent		Kanazawa et al. 2000
Oceania				
Orrak		Late Mid. Holocene	Palau	This study
Modern Palau (2)	48	Recent	Koror, Palau	Kanazawa et al. 1998
Early Guam (3)	24–46	Pre-contact	Guam	Hanihara 1998
Hawaii (4)	39–75	Protohistoric	Mokapu, Oahu	Hanihara 1998
Kiribati (5)	50	Recent	Tarawa Is.	Kanazawa et al. 1998
Tolai (6)	188	Protohistoric	New Britain	Matsumura 1995
Loyality Is. (7)	62	Recent	Loyalty Is.	Matsumura and Hudson 2005
Taumako (8)	–	Recent	Solomon Is	Kanazawa et al. 2000
Samoa (9)	–	Recent	Samoa	Kanazawa et al. 2000
Cook Is. 1 (10)	28	Recent	Southern Cooks	Yamada et al. 1988; Kanazawa et al. 2000
Cook Is. 2 (11)	21	Recent	Pukapuka Is.	Yamada et al. 1988; Kanazawa et al. 2000
Sahul				
Modern Australia 1 (12)	29–124	Recent	New S. Wales	Hanihara 1998
Modern Australia 2 (13)	42	Protohistoric	Pan Australia	Matsumura 1995
Modern Australia 3 (14)	101	Recent	Australia	Matsumura and Hudson 2005
PNG (15)	12–84	Recent	Pan PNG	Hanihara 1998
Melanesia Is. (16)	26–144	Recent	Pan Melanesia	Hanihara 1998
Nasioi (17)	–	Recent	Bougainville	Kanazawa et al. 2000
Kwaio (18)	–	Recent	Malaita	Kanazawa et al. 2000
Early Australia (19)	33–44	Prehistoric	S. Australia	Hanihara 1998

Note:
* A range of numbers reflects studies in which only the number of teeth measured for each dimension is reported; all others are for number of individuals. Kanazawa et al. (2000) does not report any sample sizes.

Australia (Scott and Turner 1997; Turner 1990a, b) provides the best opportunity for determining the affinities of early Palauans (Table 14.4). For UI1, 23.1 percent (3/13) of the Orrak sample are semishoveled or greater. This occurrence compares most closely with samples from early Guam (28.6 percent), Mainland and Insular Southeast Asia (e.g., Malay archipelago at 23.8 percent), and the Jomon. UI1 double shoveling was found in the low frequency of 7.7 percent (1/13) linking early Palauans with the same prehistoric groups as shoveling. Single-rooted UP1s occur at a rate of 55.6 percent (5/9) at Orrak; although there is not a wide difference between Sinodonts and Sundadonts in UP1 root number frequencies, this value is well within the Sundadont range,

Table 14.4. *Trait frequencies for Orrak and comparative samples in percent (n)*

Sample	UI1 Shovel	UI1 Doubleshovel	UP1 Root number	UM1 Enamel extension	UM1 Peg/reduced/ agenic	LM1 Deflecting wrinkle	LM1 Root number	LM2 Cusp number
Orrak	23.1 (13)	7.7 (13)	55.6 (9)	31.3 (16)	35.0 (20)	66.7 (9)	14.3 (14)	92.3 (13)
GUA	28.6 (53)	4.5 (68)	46.5 (127)	4.0 (123)	47.5 (120)	57.7 (104)	1.5 (132)	17.3 (110)
MIC	40.0 (20)	23.6 (17)	40.6 (69)	14.3 (70)	40.6 (69)	33.4 (45)	5.6 (72)	27.5 (51)
THE	31.2 (109)	19.6 (112)	51.6 (159)	26.0 (204)	16.2 (148)	45.1 (82)	9.3 (237)	37.7 (175)
BGK	50.0 (6)	33.3 (6)	63.9 (61)	43.0 (57)	16.7 (54)	52.3 (21)	9.4 (53)	29.4 (34)
THR	31.1 (74)	25.4 (59)	67.3 (107)	35.8 (109)	18.8 (128)	23.4 (47)	11.3 (133)	19.0 (100)
LVE	25.0 (4)	33.3 (3)	75.0 (8)	8.4 (24)	4.8 (21)	50.0 (2)	9.5 (21)	33.3 (9)
CAL	25.0 (4)	60.0 (5)	64.9 (57)	37.1 (54)	8.5 (59)	11.8 (17)	19.0 (42)	29.4 (34)
ANT	55.5 (9)	55.6 (9)	67.7 (62)	43.5 (62)	16.7 (66)	57.9 (19)	15.4 (52)	33.3 (45)
BUR	13.3 (15)	23.1 (13)	65.9 (138)	36.5 (126)	17.6 (142)	0.0 (14)	13.5 (37)	21.4 (28)
AND	20.0 (5)	0.0 (5)	61.0 (41)	0.0 (41)	8.9 (45)	33.4 (6)	18.2 (22)	56.3 (16)
MYE	23.8 (21)	5.9 (17)	50.0 (30)	5.4 (37)	0.0 (38)	30.8 (13)	6.0 (50)	50.0 (30)
MYJ	20.0 (40)	13.6 (22)	55.1 (205)	36.8 (198)	22 (186)	36.2 (58)	13.1 (130)	36.8 (117)
BOR	27.2 (22)	11.1 (18)	53.2 (141)	34.1 (94)	27.2 (114)	25.0 (36)	13.8 (94)	25.9 (58)
PHI	48.1 (27)	18.8 (16)	67.7 (155)	43.1 (123)	19.8 (126)	31.0 (58)	17.4 (121)	28.3 (92)
TAP	59.1 (22)	38.1 (21)	81.8 (22)	50.0 (28)	14.3 (28)	44.4 (9)	4.0 (25)	19.9 (21)
JOM	36.1 (36)	22.2 (59)	68.5 (73)	13.1 (76)	14.1 (135)	11.1 (72)	5.0 (100)	31.8 (66)
JSW	23.1 (13)	8.3 (12)	80.0 (40)	4.3 (46)	11.6 (43)	0.0 (12)	0.0 (67)	13.5 (37)
JTS	20.0 (10)	20.0 (10)	66.7 (12)	0.0 (22)	10.5 (19)	12.5 (8)	0.0 (26)	5.6 (18)
JYO	10.7 (28)	4.0 (25)	85.1 (47)	8.5 (59)	13.2 (53)	0.0 (22)	2.5 (81)	34.0 (50)
JHO	30.0 (30)	3.1 (22)	75.4 (69)	13.4 (75)	12.5 (88)	8.4 (48)	5.8 (103)	35.6 (73)
A12	28.4 (53)	5.9 (51)	90.2 (61)	44.5 (36)	50.9 (53)	42.9 (56)	6.4 (47)	52.6 (78)
ASK	65.1 (23)	40.0 (20)	79.1 (43)	31.8 (44)	17.1 (35)	29.4 (17)	4.8 (42)	8.0 (25)
AH1	0.0 (7)	0.0 (5)	85.7 (21)	17.7 (17)	11.7 (18)	0.0 (10)	0.0 (20)	63.6 (11)
AH2	34.1 (44)	23.3 (43)	82.6 (86)	45.5 (88)	26.7 (86)	18.9 (53)	11.5 (96)	24.7 (81)
CHS	77.0 (26)	79.2 (24)	66.7 (66)	62.1 (66)	24.4 (78)	29.6 (27)	14.3 (70)	16.7 (54)

(*continued*)

Table 14.4. (*cont.*)

Sample	UI1 Shovel	UI1 Doubleshovel	UP1 Root number	UM1 Enamel extension	UM1 Peg/reduced/ agenic	LM1 Deflecting wrinkle	LM1 Root number	LM2 Cusp number
HKG	53.3 (92)	42.7 (89)	61.3 (111)	57.5 (94)	31.3 (96)	23.4 (47)	18.9 (95)	27.4 (84)
ANY	89.9 (118)	32.4 (142)	69.9 (143)	57.6 (224)	32.6 (215	87.5 (8)	34.4 (172)	12.6 (103)
CNH	66.7 (9)	55.6 (9)	68.1 (47)	56.1 (41)	26.1 (46)	33.3 (12)	16.7 (30)	26.1 (23)
CTH	62.5 (8)	25.0 (8)	61.7 (47)	45.4 (33)	18.6 (43)	33.3 (15)	14.9 (47)	20.8 (24)
LBK	92.4 (13)	70.0 (10)	80.0 (30)	18.7 (32)	15.2 (32)	0.0 (2)	23.3 (30)	22.2 (18)
BRT	84.7 (13)	100.0 (7)	84.8 (92)	46.5 (73)	40.9 (93)	46.9 (32)	24.4 (86)	14.6 (48)
URG	82.1 (56)	34.0 (53)	78.9 (114)	42.9 (147)	45.7 (138)	36.0 (25)	38.9 (90)	14.3 (63)
MON	57.1 (7)	100.0 (5)	87.9 (33)	51.3 (37)	33.3 (42)	16.7 (12)	23.1 (26)	25.0 (20)
JPN	80.0 (20)	52.2 (23)	72.5 (138)	56.2 (130)	43.7 (126)	48.5 (64)	26.9 (119)	10.9 (92)
JHI	72.2 (18)	46.2 (13)	71.9 (96)	49.5 (93)	46.8 (94)	36.4 (44)	23.5 (85)	15.2 (66)
JK1	55.6 (97)	47.9 (96)	76.7 (133)	54.8 (144)	37.1 (124)	26.0 (54)	21.2 (85)	10.3 (68)
JRE	71.9 (89)	41.0 (83)	75.3 (93)	56.5 (108)	45.5 (110)	26.5 (68)	24.2 (95)	16.7 (72)
JK2	67.3 (52)	36.5 (52)	84.8 (46)	55.3 (47)	34.0 (50)	37.5 (32)	24.4 (45)	17.0 (47)
AMU	64.7 (17)	78.9 (19)	97.3 (111)	52.8 (89)	41.7 (103)	71.1 (38)	20.3 (74)	11.5 (52)
SIB	61.4 (44)	58.3 (24)	91.3 (264)	48.5 (239)	21.9 (256)	74.4 (43)	23.2 (164)	3.5 (86)
ESK	68.2 (132)	54.7 (117)	95.7 (767)	46.3 (703)	17.9 (786)	51.7 (176)	26.9 (598)	3.5 (372)
ALT	72.5 (40)	50.0 (38)	93.3 (255)	44.6 (233)	25.7 (214)	61.1 (54)	40.7 (273)	10.7 (112)
ATO	12.8 (47)	4.3 (47)	62.3 (212)	8.2 (220)	6.5 (230)	32.4 (37)	5.2 (155)	12.4 (97)

Note: GUA, Guam; MIC, Micronesia; THE, Thailand, early; BGK, Bangkok; THR, Thailand, recent; LVE, Laos and Vietnam, early; CAL, Cambodia and Laos; ANT, Annam and Tonkin; BUR, Burma; AND, Andaman; MYE, Malay archipelago, early; MYJ, Malay/Java; BOR, Borneo; PHI, Philippines; TAP, Taiwan, prehistoric; JOM, Jomon; JSW, Jomon, southwest; JTS, Jomon Tsukomo; JYO, Jomon Yoshiko; JHO, Jomon Hokkaido; A12, Ainu 1 and 2; ASK, Ainu Sakhalin; AH1, Ainu Hokkaido 1; AH2, Ainu Hokkaido 2; CHS South China 1 and 2; HKG, Hong Kong, recent; ANY, An-yang China; CNH, China; CTH, Chinese Thai; LBK, Lake Baikal; BRT, Buriat 1 and 2; URG, Urga and Mongol 2; MON, Mongol 3; JPN, Japan; JHI, Japan Hiogo; JK1, Japan Kamakura; JRE, Japan, recent; JK2, Japan Kanto; AMU, Amur; SIB, Northeast Siberia; ESK, Eskimo and Greenland; ALT, Aleut; ATO, Australia/Torres.

Sources: Derived from Turner (1990a, b), Scott and Turner (1997), and Irish (1998).

if at the low end. The Orrak sample exhibits enamel extensions at 31.3 percent (5/16), placing it closest to Insular and Mainland Southeast Asian samples; however, there is a break with the Guam (4.0 percent) and Micronesian (14.3 percent) groups that fall at the low end of expression. Similarities in frequencies among Orrak, Guam, and Micronesia continue with peg, reduced, and agenic UM3. Orrak at 35 percent (7/20) is lower than Guam (47.5 percent) and Micronesia (40.6 percent), though all are higher than samples in Turner's Sundadont group with but one exception (Ainu) (Turner 1990a). Palau and Guam, at 66.7 percent (6/9) and 57.7 percent, respectively, also exhibit high frequencies for LM1 deflecting wrinkle. Three-rooted LM1s are relatively common in the Orrak sample, occurring at a rate of 14.3 percent (2/14); this figure is closest to that seen in several Mainland and Insular Southeast Asian groups. However, as with enamel extensions, this occurrence is markedly higher than in other Micronesian samples. Finally, LM2 cusp number presents an interesting case, as Orrak is a distinct outlier with 92.3 percent (12/13) of teeth having only four cusps. This frequency is by far the highest of all comparative samples; those that are closest and the only other samples >50 percent, are Ainu (63.6 percent), Andaman Islanders (56.3 percent), and Early Malaysians (50.0 percent). New Guinea samples also have exceptionally high frequencies (i.e., 84.2 percent) of four-cusped LM2 (Scott and Turner 1997).

These comparisons confirm the Sundadont nature of the Orrak sample (Table 14.4). For six of the eight traits (UI1 shovel, UI1 double shovel, UP1 root number, UM1 enamel extension, LM1 root number, and LM2 cusp number), Orrak falls within the Sundadont range. For the two remaining traits (peg/reduced/agenic UM3 and LM1 deflecting wrinkle), the Orrak sample exhibits relatively high frequencies that fit best the Sinodont pattern. That a sample falls outside its purported group for a trait or two is not unusual given the range of variation in the expression of morphological traits. All but two comparative samples (BRT and AMU) have at least one frequency that falls within one standard deviation of the trait mean for the other group. Of the Sinodont group, seven of eighteen samples have at least three traits with frequencies in the Sundadont range; eight of twenty-three Sundadont samples have at least three in the Sinodont range.

14.3.2 Dental metrics

At the most basic level, the scatterplots show Orrak teeth to be absolutely large relative to those in other western Pacific samples. Summed average crown areas consistently place Orrak among the largest of all samples, as seen in Figure 14.1, where total mandibular crown area is plotted against that of the maxilla. Orrak is

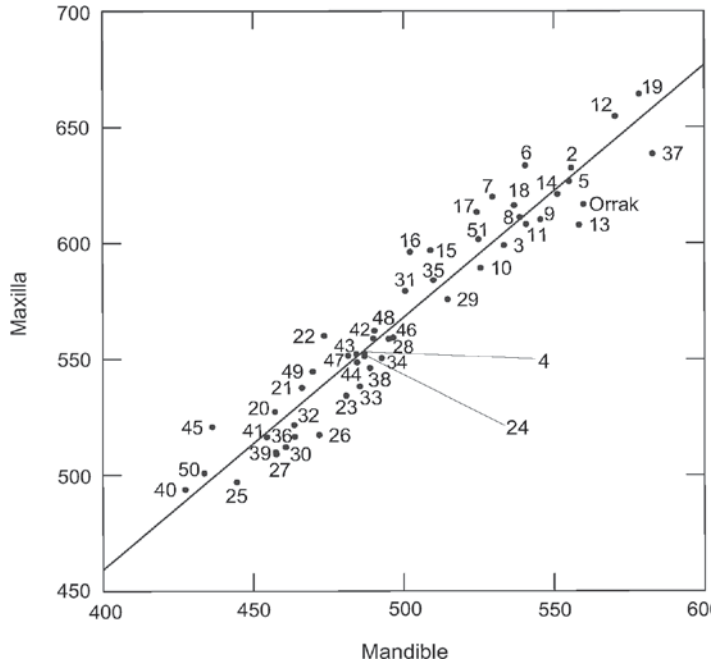

Figure 14.1. Plot of summed tooth crown areas (I1 through M2) for Orrak and a comparative sample. Number key is in Table 14.3.

at the upper end of a group representing Sahul and Oceania. This group, which includes modern Palauans, is exceeded in size by only two Australian samples and one middle Holocene sample (Malaysian Guar Kepah).

In comparison to samples of prehistoric and modern peoples compiled by Brace and Hinton (1981), Brace et al. (1990), and Hanihara (1998), the teeth from Orrak are the fourth largest for summed total crown area (Table 14.5). This highlights the fact that Orrak generally falls with groups in which dental reduction has minimally progressed. It is interesting that large tooth size is coupled with dramatic hyponconulid reduction on LM2 (92.3% 4 cusped), as the crowns are larger than those of all groups except those from Australia.

Principal component analysis (PCA) produced two factors with eigenvalues greater than 1.0 (Table 14.6); they account for 80.3 percent of the variance. Not surprisingly the factors measure tooth width, that is, Factor 1, and tooth length, Factor 2. However, on closer examination, the four highest loadings in Factor 1 are all molar measurements; thus, this factor appears to be driven by molar width. In contrast, Factor 2 appears to be driven by premolar length; three of the four highest loadings are for these measures.

Table 14.5. *Summed total crown area in mm² (I1 through M3)*

Australia, Early#	1,494
Australia, Modern#	1,489
Australia, Murray Basin**	1,429
Orrak	1,422
PNG, Eastern Highlands*	1,395
Tonga*	1,371
Malay Peninsula Mesolithic*	1,370
Bougainville Nasioi*	1,359
Flores Mesolithic*	1,358
New Britain**	1,355
Guam, Early#	1,343
Fiji*	1,338
PNG#	1,336
New Britain*	1,334
Island Melanesia#	1,333
New Hebrides*	1,328
PNG, Sepik River*	1,321
SE Asia#	1,313
Borneo Neolithic*	1,312
Guam**	1,311
Samoa*	1,311
Guam*	1,309
New Hebrides, Malekula*	1,295
Philippines, Visayas*	1,288
Celebes Mesolithic*	1,288
Bali Bronze Age*	1,287
PNG, North Coast*	1,286
New Ireland*	1,266
Bismark Archipelago*	1,259
Oahu Mokapu#	1,259
Easter Island**	1,256
New Caledonia*	1,256
Thailand Neolithic*	1,252
Japan, Recent#	1,248
New Ireland**	1,245
Java*	1,240
China Neolithic**	1,236
Thailand*	1,233
Filipino#	1,233
Yayoi, Doigahama**	1,232
Japanese**	1,229
Thailand Bronze Age*	1,224
China, North**	1,223
Thailand Neolithic**	1,222
Thailand**	1,222
Taiwan Prehistoric*	1,205
Jomon, Early**	1,211

(*continued*)

Table 14.5. (*cont.*)

Marquesas*	1,204
Thailand, Early#	1,201
Japan*	1,200
Hawaii*	1,200
Chinese#	1,192
China Bronze Age*	1,191
Borneo*	1,190
China, South**	1,187
Moriori*	1,181
Hawaii**	1,176
Vietnam**	1,169
Jomon#	1,158
China*	1,157
Jomon, Middle**	1,152
Dayak#	1,151
Ainu#	1,136
Maori**	1,135
Jomon, Late**	1,134
Negrito#	1,094
Ainu**	1,083

Note: Orrak compared to modern and archaeological samples.
Sources: Derived from Brace and Hinton (1981, noted with *), Brace et al. (1990, noted with **), and Hanihara (1998, noted with #, males only).

Discriminant analysis reveals that Orrak groups with other samples from Oceania. A plot of the first two factors (Figure 14.2) locates Orrak within the Oceania group; it also shows that Oceania and the Sahul are distinct from the other Asian groups (Factor 1) and each other (Factor 2). The first (50.2 percent) and second (33.4 percent) discriminant factors account for 83.6 percent of the dispersion. Backward stepwise modeling reveals that the first factor is driven primarily by maxillary premolar size; the second is driven by overall molar size, particularly that of the LM1s. This result, to a large degree, mirrors that of the PCA, though the factors are switched. For all dimensions, means for the Sahul and Oceania groups are larger than for the other four areas. Although Factor 1 appears to be related to upper premolar size, it more accurately reflects overall tooth size. Factor 2 also distinguishes Oceania and Sahul, though to a lesser degree than the first factor. Factor 2 appears to reflect molar size, where for the eight molar dimensions, Sahul is the largest for seven (Table 14.7).

The between groups F-matrix (Table 14.8) concurs with the discriminant factor plot and shows that mainland and insular Asian samples are closer to each other than to Sahul or Oceanic groups. It also emphasizes how different

Table 14.6. *Principal components analysis rotated (varimax) factor loadings*

Tooth	Measure	Factor 1 Loading	Factor 2 Loading
LM1	BL	**.9086**	.2164
LM2	BL	**.8401**	.4268
UM1	BL	**.8164**	.3665
UM2	BL	**.8060**	.4806
LP2	BL	.7894	.5014
UI1	BL	.7809	.4756
UI2	BL	.7719	.4234
UC	BL	.7707	.4874
LM2	MD	.7626	.5118
LC	BL	.7109	.5287
UI1	MD	.6735	.5258
LI1	BL	.6547	.5413
LP1	BL	.6438	.4641
UP2	BL	.6416	.6627
LM1	MD	.6406	.5986
UI2	MD	.6334	.4315
UP1	BL	.6051	.6862
LI2	BL	.5869	.6280
LC	MD	.5823	.7282
LP2	MD	.5497	.7770
UM1	MD	.5052	.7466
UP2	MD	.2952	**.9143**
UP1	MD	.2707	**.8671**
LP1	MD	.4903	**.8234**
UC	MD	.4989	**.8021**
LI2	MD	.4003	.7170
UM2	MD	.4809	.7164
LI1	MD	.4769	.6571
Percent of variance		41.9735	38.3243
Total variance explained by first two components 80.2978 percent			

Sahul and Oceania are in their pattern of tooth size. Though both are absolutely larger dentally, the F between them is larger than that between all others except that between Sahul and Japan.

14.4 Discussion

The analysis of dental morphology supports findings based on genetics (Lum and Cann 1998, 2000; Su et al. 2000) and language (Gray and Jordan 2000;

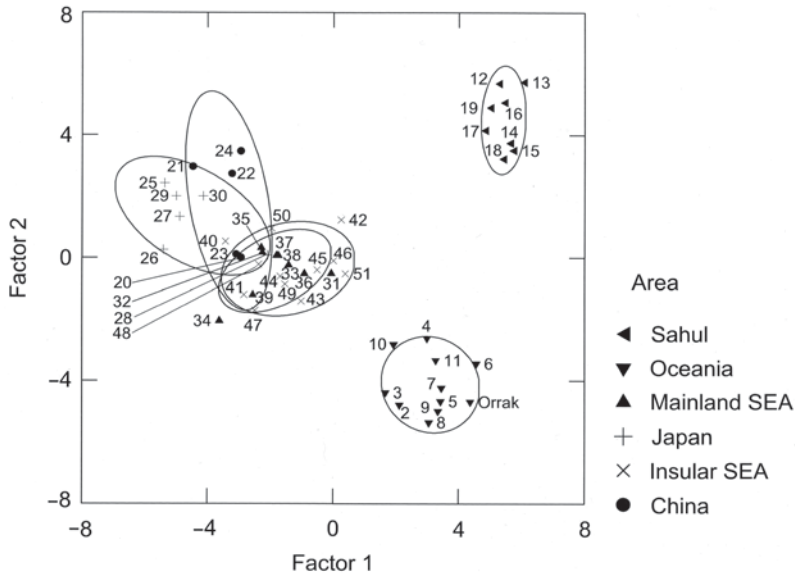

Figure 14.2. Scatter plot of first two discriminant factors. Confidence ellipse is sample based with probability set at .683 (default for Systat 7). Number key is in Table 3.

Lum and Cann 1998; Pawley 2007) that identify insular Southeast Asia as the probable point of origin for the early inhabitants of Palau. Linking Palau with the greater Sundadont group points to this area as the homeland for the earliest settlers of the archipelago; dental morphological studies by Turner and colleagues (Scott and Turner 1997; Turner 1990a, b) place the origins of the modern Sundadont group within mainland and insular Southeast Asia. Specifically, Turner (1990a) presents evidence that the Sundadont pattern evolved locally during the late Pleistocene in mainland Southeast Asia and is the ancestral condition to both the Sinodont and Australian/Melanesian patterns. In his study of dental anthropology of early Guam, Turner (1990b) finds that early inhabitants are most closely related to, in descending order, other Micronesians, Polynesians, Southeast Asians, and then Melanesians. He suggests that Borneo, through the Celebes and Moluccas, is a likely area of origin for these peoples over the Philippines and Taiwan. Finally, Scott and Turner (1997) place their Micronesian sample within the Sunda Pacific group, which also includes samples from early and recent Southeast Asia and Polynesia.

The pattern of variation in dental metrics also suggests that mainland/insular Southeast Asia is the area of origin for the earliest Palauans. Although less obvious than dental morphology in assessing affinities, the metric analysis places Orrak with its neighbors in Oceania and separates them from the other

Table 14.7. *Dental metrics; mean and standard deviation for comparative sample groups*

	China		Japan		Mainland SEA		Insular SEA		Sahul		Oceania	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Mesiodistal diameters (mm)												
UI1	8.41	.14	8.50	.26	8.57	.35	8.55	.27	9.12	.29	8.89	.27
UI2	7.15	.16	7.10	.21	7.11	.31	6.98	.30	7.37	.21	7.25	.23
UC	7.87	.17	7.70	.34	7.89	.26	7.89	.26	8.29	.16	8.45	.23
UP1	7.28	.18	7.09	.37	7.43	.29	7.33	.28	7.53	.13	7.63	.22
UP2	6.78	.19	6.63	.35	6.83	.30	6.91	.20	7.14	.21	7.29	.26
UM1	10.31	..06	10.31	.30	10.64	.32	10.59	.26	11.19	.19	11.04	.28
UM2	9.73	.30	9.53	.49	9.66	.55	9.66	.32	10.58	.36	10.41	.33
LI1	5.44	.24	5.32	.14	5.41	.25	5.40	.29	5.69	.13	5.61	.19
LI2	5.99	.17	5.88	.24	6.19	.31	6.06	.30	6.43	.13	6.29	.20
LC	6.98	.12	6.82	.27	7.07	.18	6.99	.25	7.39	.13	7.36	.18
LP1	7.05	.14	7.03	.32	7.22	.33	7.15	.24	7.47	.11	7.57	.21
LP2	7.03	.12	7.08	.32	7.27	.39	7.15	.21	7.58	.14	7.70	.24
LM1	11.24	.10	11.50	.25	11.81	.38	11.49	.36	12.03	.28	12.21	.29
LM2	10.69	.12	10.86	.34	10.87	.60	10.65	.39	11.71	.62	11.62	.29
Buccolingual diameters (mm)												
UI1	7.23	.04	7.28	.26	7.32	.31	7.30	.32	7.79	.21	7.73	.20
UI2	6.62	.11	6.59	.22	6.62	.35	6.46	.43	6.95	.13	7.01	.14
UC	8.38	.12	8.12	.30	8.38	.29	8.19	.42	9.00	.24	8.84	.15
UP1	9.53	.07	9.36	.34	9.64	.36	9.58	.23	10.17	.31	10.20	.14
UP2	9.38	.20	9.15	.36	9.46	.31	9.38	.26	10.20	.22	10.06	.18
UM1	11.76	.27	11.65	.28	11.91	.48	11.66	.39	12.50	.36	12.20	.34
UM2	11.68	.15	11.50	.29	11.81	.55	11.53	.45	12.73	.51	12.36	.40
LI1	5.80	.15	5.93	.13	5.94	.40	5.90	.29	6.37	.21	6.32	.19
LI2	6.20	.19	6.20	.20	6.37	.41	6.31	.31	6.62	.19	6.68	.17
LC	7.80	.21	7.56	.32	7.86	.37	7.70	.43	8.29	.19	8.21	.20
LP1	8.15	.11	7.85	.33	8.26	.34	8.01	.27	8.45	.77	8.66	.10
LP2	8.34	.22	8.33	.32	8.55	.28	8.31	.28	9.02	.20	8.96	.19
LM1	10.83	.13	11.02	.24	11.03	.31	10.70	.27	11.47	.41	11.20	.24
LM2	10.45	.15	10.44	.22	10.49	.34	10.21	.33	11.22	.45	11.03	.31

Table 14.8. *Between groups F-matrix*

	China	Japan	ISEA	MSEA	Sahul	Oceania
China	0.0					
Japan	0.8672	0.0				
ISEA	1.0678	1.7785	0.0			
MSEA	1.0914	1.4019	0.8629	0.0		
Sahul	4.0444	5.6373	5.1563	4.9595	0.0	
Oceania	4.1067	5.1481	3.4430	3.2435	5.3144	0.0

samples. As the F-matrix shows (Table 14.8), Oceanic samples are closer to mainland and insular Southeast Asians than to any other groups, though they are still separated by a notable margin. That Orrak groups with relatively large toothed peoples from Oceania and the Sahul probably has more relation to diet and subsistence and the concomitant lack of dental reduction in these two groups than with shared ancestry. In fact, the difference between the Sahul and Oceanic groups may actually indicate differing ancestry. In Table 14.7, the Sahul group is characterized by large molars (seven of eight dimensions are largest), while the Oceanic group displays the largest premolar dimensions (five of eight measures). This difference appears to account for the divergence between Oceania and Sahul in the second discriminant factor. This hint of different ancestral pathways for Sahul and Oceania is not very surprising given that the Sahul samples are likely made up of descendants of much earlier migrants than those who settled Oceania (i.e., the Austronesians).

Beyond determining that the origins of earliest Palauans may be found in greater Southeast Asia as an outgrowth of the seafaring Austronesian expansion, it is difficult to unravel how settling the archipelago is related to this diaspora. Whether reached accidentally or purposefully, the islands of the main Palauan Archipelago – stretching from Anguar in the southwest to Kayangel in the northwest – were probably encountered more than once by early seafarers. It is possible that Palau was visited during the early phases of the Austronesian migration out of Taiwan, as evidenced by the fact that giant swamp taro (*Cyrtosperma chamissonis*) pollen is present deep in the Ngerchau core (474 cm) (4291–4437 cal. BP, Athens and Ward 2001). The timing of this possible settlement attempt corresponds with the earliest evidence of Austronesian occupations south of Taiwan in the Batanes Islands at 4450–4080 BP (Bellwood and Dizon 2005) and the northern Philippines possibly as early as 4800 BP (Bellwood 1997; Spriggs 1999; Tsang 2007). Occupations in Palau at this time would place the origin in the northern Philippines, where Proto Malayo-Polynesian developed out of Proto Austronesian, red slipped pottery (considered an Austronesian marker) is found, and giant swamp taro added to the horticultural base (Bellwood 2004; Pawley 2007; Tsang 2007). Until archaeological evidence corroborates human presence between 4500 and 4000 BP (Athens and Ward 2001; Wickler 2001), confirmation of long-term habitation before 3500 BP is lacking. At present, it appears that permanent human settlement in Palau was not established until after 3500 BP (Clark 2005; Liston 2005); this founding likely involved peoples being sampled at sites such as Orrak and its contemporary, Ulong (Clark 2004, 2005), where red slipped pottery is present in the basal layers.

One problem in determining population affinities of Palau is that most studies combine biological markers from remains in the archipelago with other

island groups as part of a "Micronesian" sample. Whether due to small samples from any one island or a misconception that the islands of greater Micronesia represent one culture and history, it is difficult to tease out the actual human biological signature of Palau. It is apparent that the settlement history of western Micronesia, Palau and the Mariana Islands, is different than that of central and eastern Micronesia. The peoples of Palau and the Marianas both speak Western Malayo-Polynesian subgroup languages of Austronesian; those of eastern Micronesia belong to the nuclear Micronesian subgroup of Oceanic. This fact, along with dental morphometric and archaeological evidence, indicates that Palau and the Marianas were originally settled from the west, whereas central and eastern Micronesia were settled from the south (the Bismarcks) and southeast (Polynesia) by later migrants (Intoh 1997; Anderson 2003). With this scenario in mind, it is imperative that Palau be treated as a separate entity when possible; genetic, skeletal, and dental data for it and the Marianas should not be combined with each other or with material from Micronesia if we are to get a true idea of how prehistoric and modern Palauans are related to regional populations.

14.5 Conclusion

Analysis of dental remains from Chelechol ra Orrak indicates these early Palauans are most closely associated with their temporal and spatial neighbors. Orrak is morphologically most akin to other Micronesians, Southeast Asians, and Polynesians that express a Sundadont dental pattern; they are metrically closest to other Oceanic samples. As the only study that treats Palau as a separate entity, this analysis supports results from previous dental (Scott and Turner 1997; Turner 1990b), craniometric (Pietrusewsky 1990), linguistic (Gray and Jordan 2000), and DNA (Lum and Cann 1998, 2000; Su et al. 2000) analyses that place the origins of the earliest Micronesians in insular Southeast Asia.

At present, it is difficult to be more specific concerning the origins of people who established the first well-documented permanent settlement in Palau after 3500 BP. However, the close relationship between the Orrak sample and those from Borneo and Java indicates the place to search may not be in the Philippines, where western Micronesian origins have traditionally been placed; instead, the largely unsampled area of central Island Southeast Asia and the Moluccas should be explored, as Spriggs (2007) notes. As we learn more about the movements of pre-Lapita peoples around Insular Southeast Asia, it becomes apparent that with their ability to traverse long distances rapidly, interisland movements were probably fluid. This fluidity, combined with probable small population sizes – in which biological markers and language can both evolve

rapidly – and a compressed temporal window of a few hundred years make pinpointing migrant homelands difficult. However, analysis of skeletal series from large cemetery sites such as Orrak and Teouma, Vanuatu (Bedford et al. 2006; Bentley et al. 2007), will go a long way toward clarifying the biological relationships of these far ranging, early Austronesians.

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15 *Grades, gradients, and geography: a dental morphometric approach to the population history of South Asia*

BRIAN E. HEMPHILL

15.1 Introduction

The purposes of this chapter are threefold. First, it will be demonstrated that dental observations from archaeologically derived and modern samples can be combined without introducing systemic bias that compromises attempts to reconstruct population history. Second, it is shown that dental morphological trait frequencies yield similar, but distinct patterns of intersample phenetic affinities compared to those obtained with dental metrics. Third, it will be tested whether South Asians evidence long-standing local continuity, or whether they, and Pakistanis in particular, experienced significant gene flow from outside populations.

15.1.1 Relative proportionality, tooth size gradients, allocation of permanent tooth size

In recent years, largely as a consequence of the influential work of Christy Turner II, researchers interested in understanding patterns of human microevolution in the post-Pleistocene era have focused their attention on the assessment of variation in dental morphological trait frequencies. Odontometric data have been used far less commonly for the same purpose (T. Hanihara 2008; Harris 1998; Harris and Harris 2007; Harris and Rathbun 1989, 1991; Hemphill 1991, 2008, 2009b; Hemphill et al. 1992, in press).

Multivariate studies consistently demonstrate that isometric scaling accounts for a large proportion of the size variation across populations (Harris 1998;

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Harris and Rathbun 1991; Hemphill 1991; Hemphill et al. 1992). In fact, so great are differences in overall tooth size and so extensive is evidence for post-Pleistocene reduction that many researchers have concluded odontometric data are of little use for investigating microevolutionary questions (e.g., Cadien 1972; Harris and Bailit 1987; Lasker and Lee 1957; O'Rourke and Crawford 1980; Pedersen 1949; Thomsen 1955).

Isometric scaling is not the only form of odontometric variation found among modern humans. Human groups also differ in tooth size proportions within and among tooth types (de Terra 1905; Campbell 1925; Pederson 1949; Moorrees 1957). A number of studies have demonstrated that contemporary human groups possess dentitions of different shapes in the sense that "shapes" reflect differences in the proportionality of various dental elements (Rosenzweig 1970; Garn et al. 1966a, b, 1969, 1971). Since the end of the Pleistocene, not only have various human groups experienced greater or lesser amounts of overall reduction in tooth size, but the distribution or allocation of size differs across the various morphogenetic fields (K. Hanihara 1976; Harris and Rathbun 1989, 1991). Following the rationale of Penrose (1954), who noted that it is typically shape rather than size that most effectively distinguishes groups, Corruccini (1973) argued that shape is the more important determinant of dissimilarity among closely related populations. This view has been confirmed by other metric data (Campbell 1978; Corruccini 1978, 1987; Relethford 1984; Thorpe and Leamy 1984), as well as by analyses of differential allocation of tooth size throughout the dentition (Groeneveld and Kieser 1987; Harris 1998; Harris and Rathbun 1989, 1991; Hemphill 1991; Perzigian 1984).

If one assumes that variation in tooth size and size proportionality in contemporary groups has developed through divergence over time, such divergence may be the consequence of historical contingency (Gould 1991a, b). That is, intergroup differences in tooth size allocation, while statistically significant (Harris and Rathbun 1991; Perzigian 1984), may simply reflect genetic drift and gene flow. It may be that the "gradients" (Harris and Harris 2007) of tooth size across morphogenetic fields of the permanent dentition may be less subject to the selective pressures that have accompanied technological and dietary changes throughout the Holocene than the morphological traits upon which so many recent studies of biological distance are based.

15.1.2 Population history of South Asia

Recent mtDNA amplification and Y-chromosome analysis have ignited a spate of research into the biological affinities of the castes and tribes of India, their relation to the population of Pakistan, and their connections to the peoples of

neighboring Central Asia, Iran, Nepal, Southeast Asia, and beyond. As a consequence, several different models for the population history of South Asia have emerged.

An array of genetic studies suggest the Indian subcontinent served as a major corridor for the dispersal of early modern humans out of Africa into East Asia, Southeast Asia, and beyond (Barnabas et al. 2006; Basu et al. 2003; Chaubey et al. 2007; Kivisild et al. 2003; Templeton 2002). Some suggest that the population history of the myriad ethnic groups of South Asia was the product of initial colonization in the Pleistocene followed by long-standing *in situ* continuity of local populations (Kivisild et al. 2003; Metspalu et al. 2004; S. Roychoudhury et al. 2000; Sengupta et al. 2006). Some proponents of what may be termed the Long-Standing Continuity Model (LSCM) maintain that the Hindu Kush and Himalayan Mountains served as effective barriers that discouraged any subsequent and significant introduction of new genes into the subcontinent (Sahoo et al. 2006; but see Krithika et al. 2009). Noting that the majority of Indian haplogroups reflect 10,000–15,000 years of isolation, other LCSM proponents assert these ages attest to the antiquity of regional differentiation, thereby ruling out any major migratory events *within* the subcontinent since the end of the Pleistocene (Kennedy et al. 1984). Consequently, patterning of biological affinities may be a reflection of simple isolation by distance (Epperson 1993; Manel et al. 1993; Sokal and Wartenburg 1983), in which marital partners were preferentially recruited nearby. Hence, with the passage of time, populations closest temporally and geographically should be most similar biologically.

A second model may be identified as the Early Intrusion Model (EIM). Proponents of this model, such as Renfrew (1987, 1996), claim the development of agriculture in South Asia signals entry into the subcontinent of a population of farmers from western Eurasia. Once designated as the "Neolithic Arya" hypothesis, to accommodate the discovery of agricultural production in aceramic Neolithic levels at Mehrgarh, this model has lost support to a later entry, perhaps at the beginning of Period III (c. 4500 BC), when the rich burials of the Neolithic gave way to a major change during the Chalcolithic occupation of the site, where only simple burials with a few ornaments are the norm (Jarrige 1984; Jarrige and Lechevallier 1979).

Recent genetic studies have revisited debates over the origins of the hypothetical proto-Elamo-Dravidian language, which is thought by some to be the precursor of the Dravidian languages spoken in South India today. McAlpin (1981) proposed that speakers of proto-Elamo-Dravidian spread eastward from southwestern Iran with agriculture. A recent study of mtDNA among southwestern Asians, Central Asians, and Pakistanis by Quintana-Merci and coworkers (2004) found the gene pool of the Dravidian-speaking Brahui of

Pakistan to be more like that of Indo-Iranian speakers than Dravidian peakers of South India. These researchers interpret this evidence to support an external source for Dravidian populations and they identify this source as southwestern Iran. Drawing from the work of Witzel (1999), proponents of the Early Intrusion Model suggest that prior to the fifth millennium BC, inhabitants of much of the Indian subcontinent – including the Indus Valley – were speakers of proto-Mundic languages. Following McAlpin (1981) and others, they suggest proto-Elamo-Dravidian speakers entered the subcontinent from the northwest during the fifth millennium BC (Fairservis and Southworth 1989; Southworth 1995).

Historically the most influential model is the Aryan Invasion Model (AIM). Proponents of the AIM assert that Indo-Aryan languages were introduced to the Indian subcontinent during the second millennium BC by Aryan invaders from the steppes of Central Asia, whose descendants subsequently spread Vedic culture, first to the Upper Doab region of North India, then throughout the rest of the Indian peninsula (Erdosy 1995; Kuzmina 1998; Parpola 1995). Erdosy and Parpola claim the urban populations of Bactrian-Margianan Archaeological Complex (BMAC, *aka* "Oxus Civilization) are the sources of this invasion into South Asia.

In recent years, the AIM has received considerable support from genetic studies that assess the patterning of variations in mtDNA, Y-chromosome, and autosomal markers. In reviewing these data, Bamshad and coworkers (2001) found a consistent pattern of west Eurasian variations; they occurred at higher frequencies in (1) Indo-Aryan-speaking North Indians rather than Dravidian speakers of South India, (2) caste Hindus of both regions compared to non-caste tribal populations, and (3) North Indian males compared to females. Their results indicated a relatively recent immigration into the Indian subcontinent of a population of western Eurasians – possibly from Central Asia – comprising the bulk of the North Indian population, especially high-status Hindus. In a study of Y-chromosome variants, Wells and coworkers (2001) drew attention to the distribution of the paternal haplogroup R1a. Found predominantly in the Indus Valley, the Upper Doab, and Gangetic plain, this haplogroup has been identified as the "smoking gun" of the incursion of Central Asians, often associated with Indo-Aryans of the mid-2nd millennium BC (Cordaux et al. 2004).

This investigation seeks to augment genetic studies of South Asian population through the use of dental variables. Three important questions are addressed:

1. Are systemic biases introduced when prehistoric archaeologically derived samples are considered in the same analysis as samples of contemporary living individuals?

2. Does variation in dental morphological trait frequencies yield results consistent with those obtained from the assessment of tooth size allocation?
3. Is the population history of South Asia one of long-standing regional continuity, or has the population of South Asia in general, and of Pakistan in particular, been impacted by significant disturbances of local gene pools by gene flow from populations outside South Asia?

15.2 Materials and methods

15.2.1 Dental morphology

The first phase of this investigation is based on assessment of permanent tooth crown and root morphology. Dental traits were scored in accordance with the standards of the Arizona State University Dental Anthropology System (Scott and Turner 1997; Turner et al. 1991). Where possible, the dentition of each individual was assessed for 26 dental traits scored as 71 tooth-trait combinations. Observations were made on both right and left antimeres. Frequencies of dental traits were calculated for each grade of expression according to the individual count method of Scott (1973, 1980; see also Scott and Turner 1997), in which the greatest degree of expression, regardless of side, was considered the score for that individual under the assumption that this procedure reflects the maximum genetic potential for each trait (Turner 1985; Turner et al. 1991).

Trait selection is a critical issue in any biological distance analysis (Harris and Sjovøld 2004; Irish 2010; Sjovøld 1977:31). The most discriminating variables differ with the array of samples considered. Two important issues arise when such an analysis involves both living and archaeologically derived prehistoric samples. First, sample sizes are usually relatively small, and trait representation is often biased when archaeologically derived samples are considered. This is due to the limited preservation of ancient remains, the nonrandom greater postmortem loss of anterior teeth from skeletonized remains, and heightened levels of tooth wear among ancient peoples. Second, because it is unlikely that individual traits, let alone the expression of individual traits on various teeth, are controlled by separate genes or separate batteries of genes (see Keene 1991; Mitsiadis and Smith 2006; Nichol 1989; Osborn 1978; Townsend et al. 2009), it is important to determine whether specific tooth-trait combinations are intercorrelated, thereby leading to artificial inflation of intergroup differences (Sjovøld 1977).

The two-step trait editing procedure recommended by Irish (2010) and Harris and Sjovøld (2004) is followed here. The original battery of 71 tooth-trait

combinations was analyzed in raw form (in which trait expression is scored by ordinal grade of expression) for assessment of intertrait correlations with Kendall's *tau*-b correlation coefficient among all samples of living individuals. Assessment of intertrait correlations was limited to living samples because of the greater sample sizes available and the lesser degree of missing data that plague archaeologically derived samples. All tooth-trait combinations found to be significantly correlated ($\tau_B > 0.5$) were removed from further consideration. The second step tested the noncorrelated tooth-trait combinations for significant among-group differences. Traits considered to contain "contributing information" were those that exhibit "a statistically significant difference between at least one pair of the groups being evaluated" (Harris and Sjovøld 2004: 91).

Once intercorrelated and insufficiently variant tooth-trait combinations were removed, the remaining battery of ordinally graded trait expressions was dichotomized into presence/absence only for comparative purposes, where any degree of expression was considered a positive manifestation. The only exception is shoveling of the maxillary anterior teeth, where grade 2 was considered the minimum level of positive expression. Because numerous studies have found minimal sex dimorphism in trait expression (T. Hanihara 1992, 2008; Irish 1998; Scott 1973, 1980; Smith and Shigey 1988), males and females were pooled for comparative purposes.

Frequencies of sex-pooled dental morphology trait frequencies from Period 2 (3385–2920 BC: Dyson and Lawn 1989:143) and Period 3 (2640–1885 BC: Dyson and Lawn 1989:143) individuals recovered from Tepe Hissar ($n_{max} = 151$) are compared to 2,091 individuals from 21 samples that include both prehistoric and living individuals (Table 15.1, Figure 15.1). Samples of living individuals include Khowars from Chitral City (Blaylock 2008; Hemphill et al. in press), the inhabitants of Madaklasht (Hemphill 2008; Hemphill et al. 2010), and Swatis of Mansehra District (Hemphill 2009b) from the Hindu Kush highlands as well as an array of samples from peninsular India. Peninsular Indian samples are from Maharashtra in west-central India, Andhra Pradesh in southeastern India, and Bengal in northeastern India. Maharashtran samples include high-status caste Marathas (MRT) (Lukacs et al. 1998; Hemphill et al. 2000), low-status caste Mahars (MHR) (Lukacs et al. 1998; Hemphill et al. 2000), tribal Madia Gonds (MDA) (Lukacs et al. 1998; Hemphill et al. 2000), and an urban mixed caste sample from Pune (RAS) (Hemphill 1991). Samples from Andhra Pradesh include high-status caste Pakanati Reddis (PNT), low-status caste Gompadhompti Madigas (GPD), and tribal Chenchus (CHU) (Hemphill 1991). The single sample from northeastern India is an urban mixed caste sample from Kolkata (BNG) (Hemphill 1991).

Table 15.1. *Samples used in the dental morphology comparison*

Sample	Abb.	Date	N_{max} [a]
Bengalis	BNG	Living	73
Chalcolithic Mehrgarh	ChlMRG	4500 BC	25
Chenchus	CHU	Living	194
Djarkutan	DJR	2100–1950 BC	39
Gompadhompti Madigas	GPD	Living	178
Harappa	HAR	2600–1900 BC	33
Inamgaon	INM	1600–700 BC	41
Khowar	KHO	Living	136
Kuzali	KUZ	1950–1800 BC	24
Madaklasht	MDK	Living	181
Madia Gonds	MDA	Living	169
Mahars	MHR	Living	195
Marathas	MRT	Living	198
Molali	MOL	1800–1650 BC	41
Neolithic Mehrgarh	NeoMRG	6500–6000 BC	49
Pakanati Reddis	PNT	Living	182
Mixed Maharashtrans	RAS	Living	68
Sapalli Tepe	SAP	2300–2100 BC	43
Sarai Khola	SKH	200–100 BC	15
Swatis	SWT	Living	182
Tepe Hissar	TH	3300–2500 BC	151
Timargarha	TMG	1400–850 BC	25
TOTAL			2,242

Note:
[a] N_{max} represents the greatest number of individuals scored for a morphological tooth-trait combination.

Prehistoric samples encompass individuals from the Indus Valley, southern Central Asia, and peninsular India. Prehistoric Indus Valley samples include Neolithic (ca. 6500–6000 BC, Jarrige 1984; Jarrige and Lechevallier 1979, 1980) (NeoMRG) (Lukacs 1986) and Chalcolithic (ca. 4500 BC, Jarrige 1984; Jarrige and Lechevallier 1979, 1980) (ChlMRG) occupants of Mehrgarh (Lukacs and Hemphill 1991), Mature Phase (2600–1900 BC, Kenoyer 1998: 17) Harappans from Harappa (HAR) (Hemphill et al. 1991), Late Bronze Age Gandharan Grave Culture (1400–850 BC, Dani 1966, 1967) inhabitants of Timargarha (TMG), and the Iron Age occupants of Sarai Khola (SKH) (ca. 200 BC, Bernhard 1969; Lukacs 1983). Prehistoric Central Asian samples derive from the Late Bronze Age BMAC urban centers of Sapalli tepe (SKH) (2300–2100 BC, Hiebert 1994) and Djarkutan (DJR, KUZ, MOL) (ca. 2100–1650 BC, Hiebert 1994) (Hemphill et al. 1998). The sole prehistoric sample from peninsular India is the Jorwe Period inhabitants of Inamgaon (1400–700 BC, Sankalia 1984), located in the west-central Indian state of Maharashtra (Lukacs 1987).

Figure 15.1. Map of dental morphology samples.

Trait frequencies were compared using Smith's mean measure of divergence (MMD) statistic with Freeman and Tukey's (1950) angular adjustment and Green and Suchey's (1976) correction for low- and high-frequency traits. Because some have questioned the utility of Smith's statistic for the estimation of population distances (Harris 2008; Konigsberg 2006; Konigsberg and Buikstra 2006), an array of recent studies have compared results of this statistic with Mahalanobis D^2 values based on tetrachoric correlations. The studies found no significant differences in either the patterning or magnitude of affinities between samples, provided sample sizes are reasonable and traits known to be correlated are either eliminated or minimized in the battery of traits forming the basis of comparison (Edgar 2004:61; Irish 2010:390–1; Sutter and Verano 2007:201).

The patterning of intersample differences reflected in the triangular matrix of pairwise Smith's MMD values was simplified with neighbor-joining cluster analysis (Felsenstein 1989; Saitou and Nei 1987), multidimensional scaling with Guttman's (1968) coefficient of alienation, and principal coordinates analysis (Gower 1966). Multidimensional scaling was accomplished in the first

three dimensions, and the goodness of fit was assessed through the degree of stress experienced in fitting the model. The symmetric matrix of Smith's MMD values was double-centered prior to principal coordinates analysis (Rohlf 2000). The first three principal coordinate axes were retained and group scores calculated along these axes. For both multidimensional scaling and principal coordinates analyses, results were ordinated into three-dimensional space, and a minimum spanning tree (Hartigan 1975) was imposed on the array of data points to ease interpretation of the patterning of intersample associations.

A compound complexity score was calculated for each sample to test whether systemic bias affects comparisons of dental morphology trait frequencies between prehistoric and living samples. A complexity score was calculated by ranking the samples relative to one another along an ordinal scale for the 18 samples included in both dental morphology and tooth size allocation analyses. In cases where more than one sample possessed a specific tooth-trait combination in identical frequencies, each sample was awarded the average rank score for the number of tied ranks involved. The compound complexity score was based on the summed rank scores for the retained 17 tooth-trait combinations. Compound complexity scores were regressed against ranked total crown area (see later discussion) and against ranked sample value on the first dimension obtained from multidimensional scaling and the first coordinate axis obtained from principal coordinate analysis with Spearman's rho (Sokal and Rolf 1995; Zar 1999).

15.2.2 Odontometrics

The second phase of this study assessed the allocation of tooth size across the permanent dentition (Harris and Bailit 1988; Harris and Rathbun 1991). Mesiodistal and buccolingual diameters of all tooth crowns, except third molars, were measured according to the standards of Moorrees (1957). Individuals recovered from Tepe Hissar (n = 139) were compared to 22 samples that include 2,159 living and prehistoric individuals (Table 15.2, Figure 15.2). Samples of living individuals include Khowars from the village of Buni (Hemphill et al. in press), the inhabitants of Madaklasht (Hemphill 2008; Hemphill et al. 2010), and Swatis of Mansehra District (Hemphill 2009a) from the Hindu Kush highlands, as well as an array of samples from peninsular India. Peninsular Indian samples are from Gujarat and Maharashtra in west-central India, and Andhra Pradesh in southeastern India. Gujarat samples include high-status caste Vaghelia Rajputs (RAJ), low-status caste Garasias (GRS), and tribal Bhils (BHI) (Lukacs and Hemphill 1993), while Maharashtran samples include an urban mixed caste sample from Pune (RAS) (Hemphill 1991). Samples from

Table 15.2. *Map of samples employed in the tooth size allocation analysis*

Sample	Abb.	Date	N
Altyn Depe	ALT	2500–2300 BC	25
Bhils	BHI	Living	208
Chalcolithic Mehrgarh	ChlMRG	4500 BC	28
Chenchus	CHU	Living	196
Djarkutan	DJR	2100–1950 BC	48
Garasias	GRS	Living	207
Geoksyur	GKS	3500–3000 BC	64
Gompadhompti Madigas	GPD	Living	177
Harappa	HAR	2600–1900 BC	26
Inamgaon	INM	1600–700 BC	38
Khowar	KHO	Living	104
Kuzali	KUZ	1950–1800 BC	31
Madaklasht	MDK	Living	191
Molali	MOL	1800–1650 BC	52
Neolithic Mehrgarh	NeoMRG	6500–6000 BC	42
Pakanati Reddis	PNT	Living	184
Vaghelia Rajputs	RAJ	Living	190
Mixed Maharashtrans	RAS	Living	70
Sapalli Tepe	SAP	2300–2100 BC	49
Sarai Khola	SKH	200–100 BC	25
Swatis	SWT	Living	190
Tepe Hissar	TH	3300–2500 BC	139
Timargarha	TMG	1400–850 BC	21
TOTAL			2,298

Andhra Pradesh include high-status caste Pakanati Reddis (PNT), low-status caste Gompadhompti Madigas (GPD), and tribal Chenchus (CHU) (Hemphill 1991).

Prehistoric samples encompass individuals from the Indus Valley, southern Central Asia, and peninsular India. Prehistoric Indus Valley samples include individuals from Neolithic (NeoMRG) (Lukacs 1986) and Chalcolithic (ChlMRG) occupants of Mehrgarh (Lukacs and Hemphill 1991), Mature Phase Harappa (HAR) (Hemphill et al. 1991), the Late Bronze Age Gandharan Grave Culture of Timargarha (TMG) and Iron Age Sarai Khola (SKH) (Lukacs 1983). Prehistoric Central Asian samples derive from the Namazga Period III (ca. 3500–3000 BC, Kohl 1992: 184) Geoksyur villages of the Tedjen Oasis (GKS) and the Namazga Period V (ca. 2500–2300 BC, Kohl 1992) urban center of Altyn depe (ALT) located on the Kopet Dagh foothill plain of Turkmenistan, as well as the BMAC urban centers of Sapalli tepe (SKH) and Djarkutan (DJR, KUZ, MOL) of the North Bactrian Oasis (Hemphill et al. in press). The sole prehistoric sample from peninsular India is the Jorwe Period inhabitants of

Figure 15.2. Map of odontometric samples.

Inamgaon, located in the west-central Indian state of Maharasahtra (Lukacs 1985).

Tooth measurements were size corrected by standardizing them against individual geometric means in samples of living populations and against sample means in prehistoric groups (Jungers et al. 1995). Differences between samples were quantified with squared Euclidean distances and the patterning of intersample differences was simplified with neighbor-joining cluster analysis, multidimensional scaling with Guttman's (1968) coefficient of alienation, and principal coordinates analysis. Results obtained by multidimensional scaling and principal coordinates analyses were ordinated into three-dimensional space and a minimum spanning tree was imposed on the array of data points to ease interpretation of the patterning of intersample associations.

Total crown areas were calculated for each sample to test whether systemic bias affects comparisons of tooth size gradients between prehistoric and living samples. Total crown area was calculated by multiplying mesiodistal by buccolingual diameters and summing the areas from the central incisors to the second molars of the mandible and maxilla. Total crown areas were ranked along an

ordinal scale for the 18 samples included in both the dental morphology and tooth size allocation analyses. In cases where more than one sample possessed identical total crown areas, each sample was awarded the average rank score for the number of tied ranks involved. Total crown areas were regressed against ranked compound complexity scores and against ranked sample value on the first dimension obtained from multidimensional scaling as well as the first principal axis obtained by principal coordinates analysis with Spearman's rho (Sokal and Rolf 1995; Zar 1999).

15.2.3 Statistical analysis

The matrix correspondence test (Mantel 1967), a permutation procedure commonly employed to test the statistical significance of correlations between various matrices (Sokal 1979; Manly 1985), was used to assess the comparability of results obtained from dental morphology and tooth size. Such tests have often been used to test hypotheses about spatial or temporal impacts upon genetic or phenetic distances (Hemphill 1998, 1999; Hemphill and Mallory 2004; Smouse et al. 1986). Significantly high correlations between measures of biological relatedness and either geographic distances or temporal differences have been interpreted as evidence of differentiation through isolation by distance (Congdon et al. 2000; Irish 2010; Maes and Volckaert 2002; Manel et al. 2003) and/or through long-standing historical divergence (Epperson 2003; Lampert et al. 2003; Telles and Diniz-Filho 2005).

The three matrix permutation test (Smouse et al. 1986) provides additional insights into the comparability of dental morphology trait frequency and tooth size allocation data, as well as their use for the reconstruction of biological history among the eighteen samples for which dental morphology and odontometric data are available. This involved three steps. In the first step, the two triangular dissimilarity matrices were reconciled by constructing a third triangular matrix (matrix C) in which each pairwise comparison represents the absolute difference between the equivalent cells yielded by Smith's MMD statistic (matrix A) and squared Euclidean distances (matrix B). In the second step, a series of modeling matrices were constructed to determine the partial correlations between the original two dissimilarity matrices to test whether the models successfully capture the underlying correlation between them. If the model is successful, partial correlations between the two matrices after the effect of the model has been removed will be insignificant. The more successful the model, the closer the partial correlations between the two dissimilarity matrices approach to zero. In the third step, the reconciled matrix was weighted by the modeling matrices and three matrix permutation tests were used to determine

the partial correlations between the weighted reconciled matrix and the two dissimilarity matrices. When the effect of the model was held constant, and when the model was more effective in capturing the commonality between the dissimilarity matrices, the proportion of the variance between the two matrices was accounted for better.

15.2.4 Models

Four models were tested. The first tests were for pure autocorrelation. Under this model, contrasts that involve temporally distinct samples from the same locality, such as the Neolithic and Chalcolithic samples from Mehrgarh, as well as the three samples from Djarkutan, are assumed to represent population continuity at that locality. In this case, the triangular matrix of straight-line geographic distances was used as the modeling matrix, while the residuals of the partial correlations of the triangular matrices of Smith's MMD values and squared Euclidean distances were assessed with a Mantel test after 10,000 permutations.

Set theory is used to develop three additional models that take regionality into account. The regions considered here and their respective members are Tepe Hissar (TH), prehistoric Central Asians (SAP, DJR, KUZ, MOL), living populations of the Hindu Kush highlands (KHO, MDK, SWT), prehistoric inhabitants of the Indus Valley (NeoMRG, ChlMRG, HAR, TMG, SKH), prehistoric and living inhabitants of west-central peninsular India (INM, RAS), and living populations of southeastern peninsular India (CHU, GPD, PNT). Set theory provides two ways for the degree of correspondence in the results obtained by the two analyses to be evaluated.

The second model employs classical set theory. With classical set theory, group membership is such that an element (in this case, a sample) either belongs to a set (in this case, a region) or it does not. Since sets are completely bounded, between-set differences (or, in this case, differences between samples of different regions) are enhanced by multiplying reconciled absolute differences between pairs by 10, while reconciled absolute differences between samples of the same set (region) are multiplied by 1. In this case, the triangular matrix of reconciled absolute differences between Smith's MMD values and squared Euclidean distances as adjusted for within-set versus between-set contrasts that reflect *strict regionality* was used as the modeling matrix. The residuals of the partial correlations between the modeling matrix and the triangular matrices of Smith's MMD values and squared Euclidean distances were assessed with a Mantel test after 10,000 permutations.

The third and fourth models employ fuzzy set theory (Zadeh 1965). Under fuzzy set theory, sets are not completely bounded entities, but may possess

porous borders, may have overlapping ranges, or can have peripherally associated members dissociated, to varying degrees, from core members of the set. Since sets are incompletely bounded, core members of the set are weighted by 1, nonmembers are weighted by 10, while elements occupying overlapping regions or peripherally associated elements are weighted by $1 < m(x) < 10$, where m is the support or relationship of element x to the set.

In the third model, which may be termed the *strong regionality model*, it is assumed there are weak biological separations among samples within the same region coupled with strong biological separations between members of different regions. In this case, regional samples shown by both analyses to possess consistently close affinities to other samples from that same region were considered "core members." Those found by either analysis to exhibit affinities to members of other regions or to be distinctly separated from other consistently associated members of that region (i.e., "core members") were considered "peripheral members." The triangular matrix of reconciled absolute differences between pairs was dummy coded such that contrasts between samples of different regions shown by both analyses to have no interregional affinities to one another were multiplied by 10, and reconciled absolute differences between samples of the same region considered "core members" were multiplied by 1. To represent strong intraregional affinities coupled with weak inter regional affinities, the reconciled absolute differences in contrasts between "peripheral" and "core members" of a region were multiplied by 3, while contrasts between a "peripheral" member of one region to samples of the other region to which one or both of the analyses identified it as sharing affinities were multiplied by 7. The triangular matrix of reconciled absolute differences between Smith's MMD values and squared Euclidean distances adjusted for fuzzy within-set versus between-set contrasts with an assumption of strong regionality was used as the modeling matrix. The residuals of the partial correlations between the modeling matrix and the triangular matrices of Smith's MMD values and squared Euclidean distances were assessed with a Mantel test after 10,000 permutations.

The fourth model may be termed the *weak regionality model*. In this case, it is assumed there are strong biological separations among samples within the same region coupled with weak biological separations between members of different regions. "Core" and "peripheral" regional members were defined in the same way as for the *strong regionality model*. The triangular matrix of reconciled absolute differences between pairs was dummy coded such that contrasts between samples of different regions shown by both analyses to have no interregional affinities to one another were multiplied by 10. Reconciled absolute differences between samples of the same region considered "core members" were multiplied by 1. To represent weak intraregional affinities coupled

with strong interregional affinities, the reconciled absolute differences in contrasts between "peripheral" and "core members" of a region were multiplied by 7, while contrasts between a "peripheral" member of one region and samples of the other region to which one or both of the analyses identified it as sharing affinities were multiplied by 3. The triangular matrix of reconciled absolute differences between Smith's MMD values and squared Euclidean distances as adjusted for fuzzy within-set versus between-set contrasts with an assumption of weak regionality was used as the modeling matrix. The residuals of the partial correlations between the modeling matrix and the triangular matrices of Smith's MMD values and Euclidean distances were assessed with a Mantel test after 10,000 permutations.

15.3 Results

15.3.1 Dental morphology

The two-step trait editing procedure resulted in the elimination of fifty-four tooth-trait combinations. The leading factors behind elimination in order of the number of variables removed were (1) extremely low sample sizes ($n < 10$), which were especially underrepresented for third molar variants because of the sampling protocol employed for living samples (see Hemphill 2008, 2009a; Hemphill et al. 2010; in press); (2) lack of discrimination, usually due to either trait fixation or absence; and (3) intertrait correlation.

The remaining battery of seventeen tooth-trait combinations, nine maxillary and eight mandibular, was retained for comparative purposes. The maxillary variables include shoveling of UI1 and UI2, tuberculum dentale development on these same teeth, hypocone reduction on UM1 and UM2, Carabelli's trait expression on UM1, and presence of Cusp 5 on UM1 and UM2. The mandibular tooth-trait combinations include the presence of the Y-groove on LM1 and LM2 and the presence of the hypoconulid (cusp 5), entoconulid (cusp 6), and metaconulid (cusp 7) on these same teeth (Figure 15.3).

Located in the lower left corner of the array, Tepe Hissar (TH) is identified as possessing closest affinities to the BMAC samples from southern Uzbekistan. Affinities are closest with the Djarkutan Period sample (DJR) and most distant with the latest Molali Period (MOL) sample. The Molali Period sample links to prehistoric Indus Valley samples via the latest of these samples, Sarai Khola (SKH). Affinities are increasingly remote for the Late Bronze/Early Iron Age sample from Timargarha (TMG) and the Mature Phase sample from Harappa (HAR). The two pre–Mature Phase Indus Valley samples from Mehrgarh exhibit no affinities to one another or to any of the other samples from the

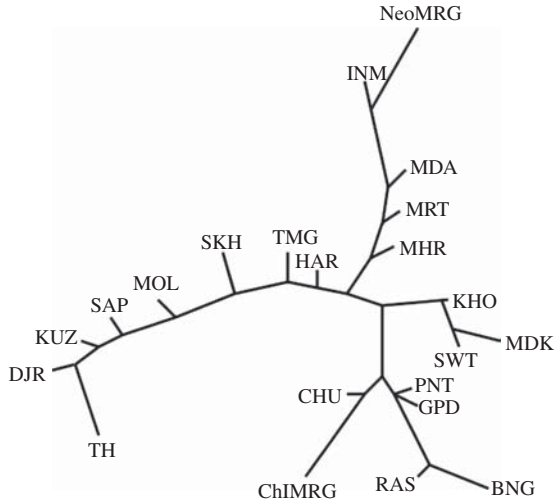

Figure 15.3. Neighbor-joining cluster analysis of Smith's MMD values based on differences in dental morphology trait frequencies for 17 tooth-trait combinations. Sample abbreviations are from Table 15.1.

Indus Valley. The earlier sample from the aceramic Neolithic levels (NeoMRG) links to samples from west-central peninsular India. This affinity is closest with the Jorwe Period sample from Inamgaon (INM) and is more remote for the living samples, but of the latter, affinities are closer with the tribal Madia Gond sample (MDA) from eastern Maharashtra than with the two Hindu caste samples (MRT, MHR). In marked contrast, the early Chalcolithic sample from Mehrgarh (ChlMRG) has closest affinities to living samples of Dravidian-speaking ethnic groups of southeast India, especially tribal Chenchus (CHU). The three samples from the Hindu Kush highlands (KHO, MDK, SWT) exhibit closest affinities to one another and have affinities intermediate between living samples from west-central and southeastern peninsular India, as well as the prehistoric Indus Valley samples from Harappa and Timargarha. The two urban mixed caste samples from Kolkata (BNG) and Pune (RAS) exhibit surprisingly close affinities to one another, followed by more distant affinities to the two Dravidian-speaking Hindu caste samples from southeast India (PNT, GPD) (Figure 15.4).

After 36 iterations, multidimensional scaling of the triangular matrix of Smith's pairwise MMD values into three dimensions with Guttman's coefficient of alienation accounts for 95 percent of the total variance (stress = 0.100). Multidimensional scaling places the sample from Tepe Hissar (TH) on the

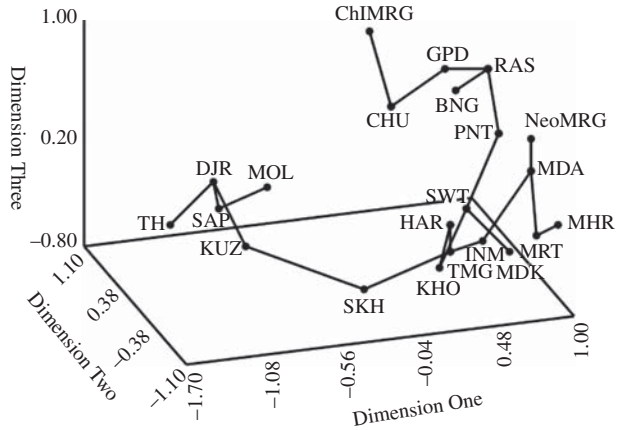

Figure 15.4. Multidimensional scaling of Smith's mean measure of divergence values based on differences in dental morphology trait frequencies for seventeen tooth-trait combinations among prehistoric and living samples with Guttman's coefficient of alienation. Abbreviations from Table 15.1.

extreme left side of the array. Tepe Hissar is identified as possessing closest affinities to the BMAC samples from southern Uzbekistan, and affinities are especially close with the Djarkutan Period sample (DJR). These samples, which are found on the left, are strongly separated from South Asian samples, regardless of whether these latter samples derive from the Hindu Kush highlands, the Indus Valley of Pakistan, or peninsular India. The only partial exception to this pattern is the latest of the prehistoric samples from the Indus Valley, Sarai Khola (SKH), which occupies an intermediate position in the center. The two samples from Mehrgarh are identified as possessing no affinities to one another. As with neighbor-joining cluster analysis, the earlier sample (NeoMRG) is identified as possessing closest affinities to inhabitants of west-central peninsular India. However, multidimensional scaling suggests that affinities are closer to living Madia Gond tribals (MDA) than to the prehistoric sample from Inamgaon (INM). Nevertheless, multidimensional scaling is consistent with neighbor-joining cluster analysis in identifying that the most distant affinities between west-central Indians and the Neolithic inhabitants of Mehrgarh occur with the two Hindu caste samples (MHR, MRT). Multidimensional scaling identifies the Chalcolithic Period inhabitants of Mehrgarh (ChlMRG) as possessing closest affinities to living Dravidian-speaking samples, especially tribal Chenchus (CHU) – a result consistent with the findings of neighbor-joining cluster analysis. The three samples from the Hindu Kush highlands are found in the lower

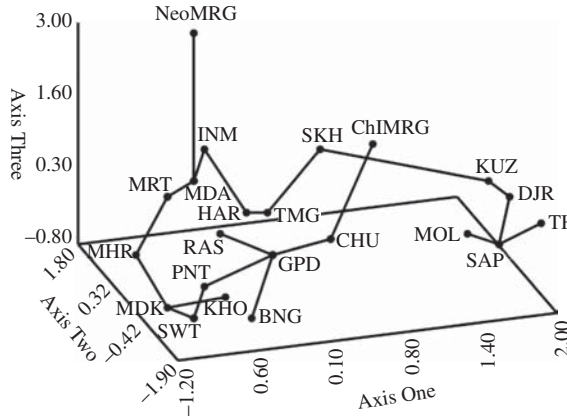

Figure 15.5. Principal coordinates analysis of Smith's mean measure of divergence values based on differences in dental morphology trait frequencies for seventeen tooth-trait combinations among prehistoric and living samples with Guttman's coefficient of alienation. Abbreviations from Table 15.1.

right. Khowars (KHO) are marked by affinities to Mature Phase Harappans (HAR) from the Indus Valley, on the one hand, and to Swatis (SWT), on the other. Swatis (SWT), and especially the residents of Madaklasht (MDK), do not share close affinities to any of the other samples, even to Khowars. The two mixed caste urban samples (BNG, RAS) occupy unexpected positions adjacent to one another among the living Dravidian-speaking samples from southeastern India (Figure 15.5).

The first three principal coordinate axes account for 88.3 percent of the total variance. Principal coordinates analysis yields results consistent with those obtained by neighbor-joining cluster analysis and multidimensional scaling. The sample from Tepe Hissar (TH) is identified as occupying a position on the extreme edge of the array, this time on the right, with closest affinities to the BMAC samples. However, unlike the previous analyses, principal coordinates analysis suggests that closest affinities are with the earliest BMAC sample from Sapalli tepe (SAP). Overall, phenetic separation between Tepe Hissar and the Central Asian samples from southern Uzbekistan is not as marked as that depicted by neighbor-joining cluster analysis or by multidimensional scaling. The latest Indus Valley prehistoric sample, Sarai Khola (SKH), occupies an intermediate position along the first axis in the center of the array, but unlike in multidimensional scaling, the Chalcolithic Period sample from Mehrgarh (ChlMRG) also occupies an intermediate position along this first axis. While the sample from Sarai Khola has affinities to two earlier prehistoric

samples from the Indus Valley (TMG, HAR), the samples from Mehrgarh are identified as possessing no phenetic affinities to one another or to any of the other Indus Valley samples. The Neolithic sample (NeoMRG) is identified as possessing closest, albeit distant, affinities to living and prehistoric inhabitants of west-central peninsular India, particularly the tribal sample of Madia Gonds (MDA) from eastern Maharashtra. The later Chalcolithic inhabitants of Mehrgarh are identified as possessing closest affinities to Dravidian-speaking inhabitants of southeastern India; in this case, affinities are closest with the tribal sample of Chenchus (CHU). Located in the lower left, the three living samples of Hindu Kush highlanders occupy a phenetic position intermediate between living and prehistoric inhabitants of west-central India, on the one hand, and living ethnic groups of southeastern India, on the other. In contrast to results obtained by neighbor-joining cluster analysis and multidimensional scaling, principal coordinates analysis indicates that it is the Khowars, rather than the Madaklasht, that stand apart from other Hindu Kush highlanders. The two mixed caste urban samples (BNG, RAS) are identified as possessing closest affinities to living ethnic groups from southeast India, but unlike results obtained from the other analyses, principal coordinates analysis does not identify these two samples as possessing closest affinities to one another. Instead these two samples occupy positions equidistant, but in opposite phenetic directions, from the low-status Dravidian-speaking Hindu caste sample of Gompadhompti Madigas (GPD).

15.3.2 Odontometric analysis

Neighbor-joining cluster analysis indicates that the sample from Tepe Hissar (TH) shares closest phenetic affinities to prehistoric Central Asians from southern Uzbekistan (DJR, KUZ, MOL, SAP) and from the Tedjen Oasis of southeastern Turkmenistan (GKS), although these affinities are not close. Remaining samples tend to aggregate by region, with several exceptions. The prehistoric samples from the Indus Valley exhibit closest affinities to one another, except for the sample from Harappa, which has closest affinities to the sample from Inamgaon (INM) located in west-central peninsular India (Figure 15.6). Affinities are particularly close between the two post-Mature Phase samples from Timargarha (TMG) and Sarai Khola (SKH). The two temporally distinct samples from Mehrgarh do not show close affinities to one another and are identified as peripheral members of the aggregate that includes the other prehistoric Indus Valley samples. The remaining samples from west-central peninsular India are marked by closest affinities to one another, except for the mixed caste urban sample from Pune (RAS), which is

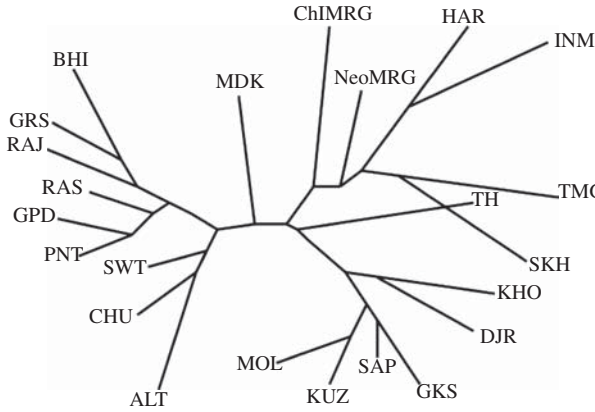

Figure 15.6. Neighbor-joining cluster analysis of squared Euclidean distances (×100) obtained from geometrically scaled mesiodistal and buccolingual diameters for all teeth, except third molars, among all prehistoric and living samples. Abbreviations from Table 15.2

identified as possessing closer affinities to Dravidian-speaking caste Hindus from southeastern India. The three ethnic group samples from the Hindu Kush highlands (KHO, SWT, MDK) possess no affinities to one another. The Swatis (SWT) are part of a three sample aggregate that also includes the sample of Dravidian-speaking tribals from southeast India (CHU) as well as the Namazga V Period sample from the Kopet Dagh foothill plain of southern Turkmenistan (ALT). As such, this aggregate includes samples separated by the greatest geographic distances. The sample from Madaklasht (MDK) is found in the center of the array and appears to share no affinities to any of the other samples. In marked contrast, Khowars (KHO) are identified as possessing closest affinities to the BMAC samples from southern Uzbekistan, as well as to the Namazga III Period sample from the Tedjen Oasis of southeastern Turkmenistan (GKS) (Figure 15.7).

Multidimensional scaling of the diagonal matrix of squared Euclidean distances into three dimensions with Guttman's coefficient of alienation accounts for 95.8 percent of the total variance (stress = 0.092) after 64 iterations. Located in the lower left of the array, multidimensional scaling identifies the inhabitants of Tepe Hissar (TH) as possessing rather distant affinities to the BMAC samples from southern Uzbekistan (DJR, KUZ, MOL, SAP) and the Namazga III Period sample from the Tedjen Oasis of southeastern Turkmenistan (GKS). Remaining samples generally fall into regional aggregates, but with exceptions. Prehistoric Indus Valley samples occupy the lower

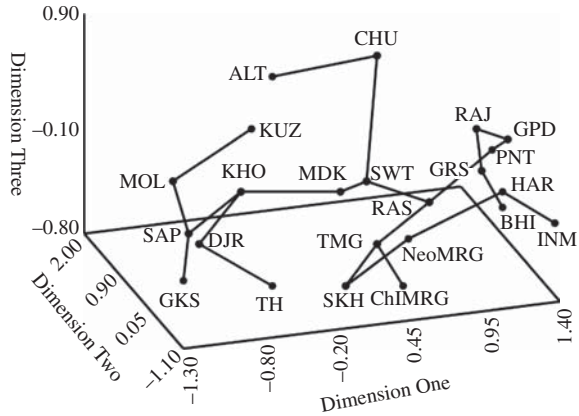

Figure 15.7. Multidimensional scaling of squared Euclidean distances (×100) obtained from geometrically scaled mesiodistal and buccolingual diameters for all teeth, except third molars, among all prehistoric and living samples. Abbreviations from Table 15.2

center with fairly close affinities between the two post-Mature Phase samples (TMG, SKH) and the later sample from Mehrgarh (ChlMRG). Affinities are somewhat more distant for the earlier sample from Mehrgarh (NeoMRG), and especially the Mature Phase sample from Harappa (HAR). The prehistoric sample from west-central peninsular India (INM) is identified as distantly associated with these prehistoric Indus Valley samples. The three living samples from west-central India (BHI, GRS, RAJ) are most similar to one another and have secondary affinities to the two Dravidian-speaking caste samples from southeast India (GPD, PNT). The mixed caste urban sample from Pune (RAS) is markedly divergent from the other living samples from peninsular India with rather distant affinities to the prehistoric Indus Valley sample from Timargarha (TMG) and the living Swatis (SWT) of the Hindu Kush highlands. The three Hindu Kush ethnic groups are identified as possessing closer affinities to one another than suggested by neighbor-joining cluster analysis. Affinities are particularly close between the Madaklasht (MDK) and Swatis (SWT), with Khowars (KHO) more distantly removed toward the phenetic space occupied by the prehistoric Central Asian samples from southern Uzbekistan. Two samples are phenetically isolated from all others: tribal Chenchus (CHU) from southeastern India and the Namazga V Period inhabitants of Altyn depe (ALT) (Figure 15.8).

The first three principal coordinate axes account for 66 percent of the total variance. Individuals from Tepe Hissar (TH) occupy a highly isolated position

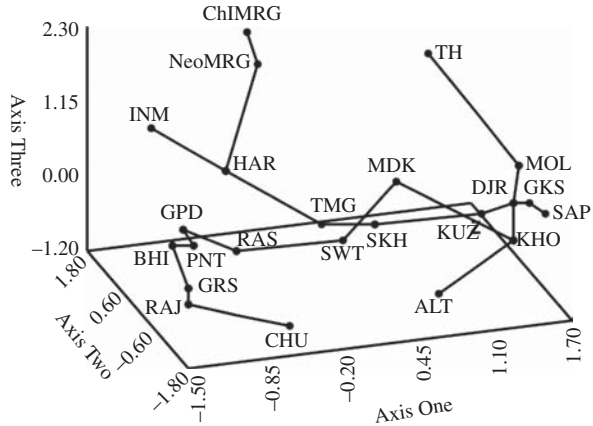

Figure 15.8. Principal coordinates analysis of squared Euclidean distances (×100) obtained from geometrically scaled mesiodistal and buccolingual diameters for all teeth, except third molars, among all prehistoric and living samples. Abbreviations from Table 15.2.

in the upper right of the array that links to the other samples by only a very distant and tenuous connection to the latest of the prehistoric BMAC samples from southern Uzbekistan (MOL). Remaining samples are largely arranged by regional aggregates, but again there are exceptions. Peninsular Indians occupy the lower left side, and for inhabitants of both Gujarat and Andhra Pradesh, affinities are closer between the two Hindu caste samples (GRS and RAJ, GPD and PNT) than to their respective tribal samples (BHI, CHU). This is especially the case for the Chenchus (CHU), who occupy a highly isolated phenetic position. The mixed caste urban sample from Pune is rather divergent from the other three living samples from west-central India (BHI, GRS, RAJ) and links peninsular Indian samples to samples from other regions via a distant connection to the Swatis (SWT) of the Hindu Kush highlands. The three samples from the Hindu Kush exhibit closest affinities to one another, but it is clear that affinities are closer, but not especially close, between Swatis and the inhabitants of Madaklasht (MDK) than either group shares with Khowars (KHO). Instead, Khowars occupy a position peripheral to the prehistoric samples from southern Uzbekistan and to the Namazga III Period sample from the Tedjen Oasis (GKS). The remaining prehistoric sample from Central Asia, Altyn depe, occupies a highly isolated position in the right foreground. Prehistoric samples from the Indus Valley are widely dispersed throughout the center and upper right. Affinities are fairly close between the two post-Mature Phase samples (TMG. SKH), as are affinities between the two samples from Mehrgarh (NeoMRG,

ChlMRG), while the Mature Phase sample from Harappa (HAR) links these pairs of prehistoric Indus Valley samples to one another. Once again, the prehistoric sample from west-central peninsular India (INM) is associated with prehistoric samples from the Indus Valley.

15.3.3 Prehistoric and living populations

Are systemic biases introduced when prehistoric archaeologically derived samples are considered in the same analysis as samples of contemporary living individuals? Ranked total crown area was contrasted against each group's ranked compound complexity score to test whether systemic bias renders comparisons between samples of ancient and living ethnic groups moot. The correlation between ranked total crown area and ranked complexity score among the eighteen samples in which data were available for both tooth size and crown complexity is 0.004, which is not significant ($p = 0.986$).

Total crown area was contrasted to the sample's ranked position on the first dimension produced by multidimensional scaling and the first principal coordinate axis produced by principal coordinates analysis with Spearman's rho. A nonsignificant relationship between total crown area and group scores obtained for the first dimension from multidimensional scaling and the first principal coordinate axis ensures that geometric scaling removes the effect of overall size but leaves disparities in the allocation of tooth size throughout the dentition to differentiate between samples. This relationship was found to be nonsignificant for both the first dimension obtained through multidimensional scaling ($r_s = -0.233$; $p = 0.351$) and the first principal coordinate axis ($r_s = 0.158$; $p = 0.530$).

Ranked compound complexity scores were contrasted to the sample's ranked position on the first dimension produced by multidimensional scaling and the first principal coordinate axis produced by principal coordinates analysis with Spearman's rho. If compound complexity scores reflect coordinated enhancement or simplification of crown complexity, then significant correlations ought to occur between compound complexity scores and group scores along the first dimension obtained from multidimensional scaling and the first coordinate axis obtained by principal coordinates analysis. Correlations between ranked compound complexity score and ranked position on the first dimension obtained by multidimensional scaling ($r_s = 0.709$; $p = 0.001$) and on the first principal coordinate axis ($r_s = -0.699$; $p = 0.001$) are both highly significant.

These results indicate two things. First, geometric scaling of mesiodistal and buccolingual crown diameters removes the impact of overall size, leaving

different proportions in tooth size to distinguish between samples with multidimensional scaling and principal coordinates analysis. Second, analysis of dental morphological variation with Smith's MMD statistic with these same two data reduction techniques differentiates among samples along coordinated vectors of crown enhancement and simplification. Thus, when such results are considered together, it is clear that no systemic bias is introduced into contrasts of dental morphology trait frequencies or allocation of tooth size when prehistoric and living samples are included in a single analysis.

15.3.4 Dental morphology and tooth size

Does variation in dental morphology yield results consistent with those obtained from allocation of permanent tooth size? The null hypothesis expects the assessment of dental morphological trait frequencies and assessment of size allocation throughout the dentition to provide information about population histories through patterning of pairwise phenetic distances between samples. If the two triangular matrices of Smith's MMD values and squared Euclidean distances are realizations of the same variation generating process, and if a significant influence upon that process is geographic propinquity, each distance matrix should be significantly correlated with geographic differences. If the observed correlation between the two is the consequence only of geography, their partial correlation after geography has been removed should be zero (Oden and Sokal 1992:280).

Three things are required to demonstrate that variation in tooth morphology yields results consistent with those obtained from allocation of permanent tooth size for reconstructing biological histories. First, there must be a significant correlation in the triangular matrices of pairwise differences between samples yielded by these two assessments of biological distance. Second, each of these matrices must be significantly correlated with a matrix of geographic distances between sample pairs. Third, the partial correlation between the matrix of Smith's MMD values and the matrix of squared Euclidean distances must be effectively zero after the effect of geography has been removed.

The degree of correspondence between the triangular matrix of pairwise Smith's MMD values (Table 15.3) based on crown trait frequencies and the triangular matrix of squared Euclidean distances based on geometrically scaled mesiodistal and buccolingual diameters (Table 15.4) was assessed with the Mantel test for the eighteen samples with both sets of data. This test yielded a t-value of 2.083, which indicates that the two matrices are not significantly different from one another ($r = 0.205$; $p = 0.981$). The degree of correspondence between the triangular matrix of Smith's MMD values and straight-line

geographic distances between sample pairs (Table 15.5) yields a t-value of 3.532, which indicates that geographic distance is significantly correlated with the divergence values yielded by crown trait frequencies ($r = 0.336$; $p = 0.999$); the likelihood of finding such correspondence by chance through 10,000 iterations is infinitesimally small ($p = 0.0026$). A similar assessment of the degree of correspondence between the squared Euclidean distances and straight-line geographic distances between sample pairs yielded a t-value of 2.983, which also indicates that the two matrices are significantly correlated ($r = 0.347$; $p = 0.999$); the likelihood of occurring purely by chance is again very small ($p = 0.0025$). However, once the effect of geography is removed, the partial correlation of the residuals yielded by the triangular matrices of Smith's MMD values and squared Euclidean distances is not significant ($t = 0.934$; $r = 0.010$; $p = 0.825$).

Results indicate that dental morphological trait frequencies and permanent tooth size allocations represent realizations of the same variation generating process. Further, both measures are significantly autocorrelated with straight-line geographic distances. Four models were developed to determine whether that autocorrelation encompasses an underlying structure.

In the first model it was assumed that there is no structure to the pattern of autocorrelation. As noted previously, straight-line geographic distances are associated with both matrices, for the correspondence between the reconciled matrix of phenetic distances and straight-line geographic distances is significant ($t = 2.470$; $p = 0.993$) and unlikely to be the result of random chance ($p = 0.009$ after 10,000 iterations). However, a three matrix permutation test with the effect of the reconciled matrix held constant indicates that pure autocorrelation explains little of the patterning ($r = 0.215$; 4.62 percent) behind the shared variation between samples. While geographic distance plays a distinct role in the biological differentiation among these samples, little of that differentiation is explained by pure autocorrelation.

Alternatively, imposition of *strict regionality* with classical set theory yields a model that couples an expectation of a high degree of phenetic homogeneity within regions coupled with a high degree of phenetic heterogeneity between regions. Thus, dental morphology and tooth size allocation data ought to reflect small distances among samples within a geographic region coupled with markedly larger biological distances between samples of different regions. The partial correlations between the Smith's MMD distances and the squared Euclidean distances after the effects of the modeling matrix of strict regionality have been removed are insignificant ($r = 0.105$; $t = 1.032$; $p = 0.844$). A test of the correlation between the dissimilarity matrix of Smith's MMD distances and squared Euclidean distances with the effects of the reconciled modeling matrix held constant are much higher ($r = 0.673$),

Table 15.3. *Mean measure of divergence analysis (MMD values below diagonal, standard deviations below diagonal)*

	BNG	ChlMRG	CHU	DJR	GPD	HAR	INM	KHO	KUZ	MDK
BNG	–	2.045	0.666	1.852	0.683	2.515	1.765	0.834	2.568	0.691
ChlMRG	9.758	–	1.744	2.904	1.761	3.572	2.828	1.913	3.618	1.769
CHU	5.542	4.854	–	1.556	0.380	2.225	1.469	0.536	2.268	0.387
DJR	21.059	10.198	7.855	–	1.574	3.405	2.624	1.704	3.450	1.579
GPD	2.929	7.134	0.540	13.000	–	2.242	1.487	0.553	2.285	0.405
HAR	6.523	5.020	4.881	13.930	5.838	–	3.268	2.372	4.061	2.247
INM	14.294	11.615	7.628	12.657	7.441	3.906	–	1.644	3.350	1.495
KHO	7.813	7.776	3.550	11.120	4.690	2.655	4.152	–	2.422	0.562
KUZ	18.282	10.082	9.961	–4.419	14.322	7.591	11.858	12.309	–	2.292
MDK	5.214	9.291	7.561	20.776	6.104	5.144	6.566	1.327	18.960	–
MDA	10.859	10.418	4.236	15.208	3.773	4.879	0.851	4.253	16.620	6.488
MHR	7.811	10.352	6.121	22.756	5.050	2.546	2.776	2.093	22.086	2.298
MRT	9.322	10.660	5.997	18.497	4.530	1.501	0.513	3.208	16.643	4.093
MOL	13.329	2.087	4.769	–2.635	9.832	4.870	11.441	5.471	–3.287	12.053
NeoMRG	19.140	6.124	11.259	16.742	11.774	6.355	–0.420	10.944	17.776	12.032
PNT	2.104	7.583	2.779	18.947	0.773	2.666	8.186	3.489	18.933	4.088
RAS	–0.521	4.835	3.974	20.778	1.865	3.339	9.570	6.707	19.114	4.275
SAP	17.556	6.455	6.912	–4.368	12.234	8.987	14.634	8.703	–5.332	17.729
SKH	21.177	14.816	7.236	5.763	9.692	2.572	–0.308	7.991	–1.490	15.799
SWT	2.520	7.428	4.858	17.146	4.152	2.484	7.360	0.552	16.479	–0.171
TH	23.835	15.351	11.203	–3.900	15.918	13.730	16.501	14.608	–3.511	24.961
TMG	13.547	8.126	3.811	8.330	5.809	–0.136	–1.345	0.092	4.076	3.943

show significant correspondence between the two ($t = 8.213$; $p = 1.0$), and are unlikely due to random chance (0.010 after 10,000 iterations). Thus, by simply imposing a model of strict regionality, the degree of correspondence between the two distance matrices is improved by nearly an order of magnitude from 4.62 percent to 45.29 percent.

In the real world, strict regionality is unlikely to exist, for even with significant geographical barriers, linguistic differences, and cultural prescriptions, population movements and avenues of genetic exchange occur, often through myriad intermediaries across great distances (Fix 1999). Fuzzy set theory offers a means to construct models that allow for varying amounts of interregional genetic exchange. A model of *strong regionality* calls for high levels of genetic exchange among "core" regional members, coupled with lower levels of exchange with "peripheral" members and members of other regions. The partial correlations between the Smith's MMD distances and the squared Euclidean distances after the effects of the modeling matrix of strong regionality have been removed are insignificant ($r = 0.103$; $t = 0.922$; $p = 0.822$). A test of the correlation between the dissimilarity matrix of Smith's MMD distances and squared Euclidean distances with the effects of the reconciled modeling

MDA	MHR	MRT	MOL	NeoMRG	PNT	RAS	SAP	SKH	SWT	TH	TMG
0.71	0.681	0.67	1.534	1.505	0.68	1.02	1.773	3.467	0.7	0.976	3.145
1.788	1.759	1.747	2.597	2.576	1.758	2.093	2.818	4.517	1.779	2.025	4.146
0.407	0.378	0.366	1.234	1.206	0.376	0.717	1.480	3.171	0.398	0.691	2.868
1.599	1.571	1.560	2.427	2.393	1.570	1.902	2.678	4.352	1.586	1.888	4.026
0.425	0.396	0.384	1.251	1.223	0.394	0.735	1.497	3.188	0.415	0.707	2.884
2.267	2.239	2.229	3.074	3.064	2.239	2.562	3.326	5.012	2.255	2.548	4.648
1.513	1.485	1.473	2.332	2.289	1.483	1.810	2.562	4.229	1.506	1.774	3.950
0.580	0.553	0.540	1.394	1.368	0.550	0.883	1.628	3.319	0.576	0.836	3.015
2.311	2.283	2.271	3.139	3.090	2.282	2.617	3.370	5.042	2.299	2.572	4.704
0.432	0.404	0.392	1.258	1.230	0.402	0.742	1.503	3.194	0.424	0.712	2.889
–	0.423	0.412	1.278	1.251	0.421	0.763	1.523	3.215	0.443	0.731	2.908
1.908	–	0.383	1.249	1.222	0.392	0.404	1.495	3.187	0.414	0.705	2.882
0.531	0.161	–	1.237	1.211	0.381	0.723	1.484	3.176	0.402	0.694	2.870
13.479	15.117	13.979	–	2.071	1.248	1.582	2.353	4.031	1.266	1.559	3.725
3.626	8.359	5.663	15.250	–	1.220	1.557	2.313	4.013	1.240	1.521	3.672
5.095	2.773	3.335	12.576	12.718	–	0.732	1.494	3.185	0.412	0.705	2.881
6.488	4.768	5.406	13.528	9.481	1.160	–	1.822	3.521	0.752	1.023	3.188
16.326	19.566	17.078	–5.141	20.681	16.255	18.726	–	4.278	1.510	1.824	3.987
5.836	9.628	4.112	6.165	9.840	11.768	18.223	3.851	–	3.202	3.486	5.602
6.551	2.536	4.466	9.004	12.286	1.879	2.737	14.046	14.990	–	0.719	2.899
18.874	25.910	21.110	0.647	21.718	21.329	24.447	–2.101	5.170	20.578	–	3.221
0.579	0.996	–0.873	4.272	4.463	6.192	10.547	7.101	–7.645	5.552	11.297	–

matrix held constant offers no improvement over the strict regionally bounded model; in fact, results are slightly worse (r = 0.663), although significant (t = 8.157; p = 1.0) and unlikely due to random chance (0.0095 after 10,000 iterations). Such results suggest that limited porousness of regional groups is an unlikely mechanism to account for the patterning of biological affinities among the post-Pleistocene South Asian and Central Asian groups included in this study.

An alternative model based on fuzzy set theory may be designated as one of *weak regionality*. Such a model calls for high levels of genetic exchange between "core" members of a region coupled with rather marked biological differences between "core" and "peripheral" members of that regional group. These differences may be the consequence of genetic drift, population bottlenecks, immigration of nonlocal regional groups, or extensive gene flow into a regional group from populations of other regions. The partial correlations between Smith's MMD distances and squared Euclidean distances after the effects of the modeling matrix of *weak regionality* have been removed are insignificant and more closely approach zero (r = 0.089; t = 0.839; p = 0.799). A test of the correlation between the dissimilarity matrix of Smith's MMD distances

Table 15.4. *Squared Euclidean distances (x100) between sample pairs*

	ALT	BHI	ChlMRG	CHU	DJR	GRS	GKS	GPD	HAR	INM
ALT	0.000									
BHI	3.890	0.000								
ChlMRG	4.225	2.584	0.000							
CHU	3.507	2.843	3.564	0.000						
DJR	3.769	3.873	3.105	3.113	0.000					
GRS	3.780	1.434	2.854	2.623	3.609	0.000				
GKS	4.589	4.215	3.500	3.650	2.657	3.942	0.000			
GPD	3.953	2.099	2.489	2.738	3.795	2.012	3.909	0.000		
HAR	4.303	2.844	2.613	3.297	3.614	3.090	3.838	2.764	0.000	
INM	5.244	2.911	2.813	4.136	4.400	3.402	4.687	3.001	2.581	0.000
KHO	3.216	3.337	2.972	2.799	1.972	2.938	2.534	3.273	3.574	4.481
KUZ	4.548	4.512	3.688	3.706	3.460	4.411	2.978	3.951	3.504	4.412
MDK	3.496	2.710	2.349	2.303	2.513	2.573	2.902	2.388	2.545	3.337
MOL	4.331	4.312	3.229	3.902	2.859	4.258	2.732	4.105	3.642	4.667
NeoMRG	3.873	2.111	1.668	2.845	2.828	2.403	3.027	2.325	2.298	2.747
PNT	4.006	2.111	2.441	2.434	3.336	1.952	3.637	1.005	2.476	2.676
RAJ	3.628	1.926	2.887	2.231	3.384	1.405	3.937	1.717	2.918	3.343
RAS	3.716	1.795	2.067	2.609	3.358	1.861	3.280	1.271	2.535	2.981
SKH	4.550	3.090	3.098	3.290	3.061	2.982	2.791	3.556	2.859	3.887
SAP	3.935	3.950	3.185	3.400	2.321	3.808	1.883	3.910	3.595	4.692
SWT	3.140	2.287	2.398	2.114	2.634	2.016	3.343	1.992	2.847	3.530
TH	3.810	3.265	2.604	3.165	2.662	3.522	3.073	3.063	3.299	4.059
TMG	4.944	3.379	3.134	3.300	3.626	3.580	3.402	3.346	2.309	3.521

and squared Euclidean distances with the effects of the reconciled modeling matrix held constant explain even more of the observed variation in the patterning of pairwise distances (r = 0.701) than the strictly bounded model. The *weak regionality model* is significant (t = 8.623; p = 1.0) and unlikely due to random chance (0.003 after 10,000 iterations).

15.4 Discussion

15.4.1 Prehistoric populations, living populations and the question of systematic bias

Are systemic biases introduced when prehistoric archaeologically derived samples are considered in the same analysis as samples of contemporary living individuals? Total crown area, as a measure of overall tooth size, was ranked by sample and regressed upon each sample's ranked complexity score as a measure of overall crown morphological elaboration to determine whether systemic bias is introduced when archaeologically derived samples are considered in the

KHO	KUZ	MDK	MOL	NeoMRG	PNT	RAJ	RAS	SKH	SAP	SWT	TH	TMG
0.000												
3.305	0.000											
2.196	2.984	0.000										
2.652	2.371	2.678	0.000									
2.752	3.249	1.937	3.083	0.000								
3.043	3.704	2.056	3.862	2.205	0.000							
2.956	4.250	2.264	4.094	2.530	1.333	0.000						
2.704	3.433	1.991	3.317	1.748	1.388	1.851	0.000					
2.723	3.617	2.533	3.189	2.231	3.321	3.210	3.013	0.000				
1.935	2.541	2.683	1.982	2.763	3.675	3.789	3.083	2.520	0.000			
2.234	3.573	1.453	3.212	2.063	1.668	1.635	1.695	3.096	3.141	0.000		
2.834	3.633	2.074	3.123	2.240	2.982	3.220	2.516	3.160	2.749	2.390	0.000	
3.422	3.028	2.892	3.344	2.621	3.120	3.436	2.864	2.313	2.888	3.428	3.184	0.000

same analysis as samples of contemporary living individuals. No correlation (r_s = 0.004; p = 0.986) was found between these two variables. Thus, there appears to be no relationship between crown size and crown complexity among the samples considered here. Ranked crown area was also regressed upon the ranked sample scores along the first dimension yielded by multidimensional scaling and by the first principal coordinate axis yielded by principal coordinate analysis. Neither of these correlations was significant, demonstrating that the effect of gross size has been effectively removed, thereby permitting assessment of differential tooth size allocation (or "gradients") across and within the morphogenetic fields of the permanent dentition (Harris and Harris 2007). Similar regressions of ranked complexity scores by sample along the first dimension yielded by multidimensional scaling and by the first principal coordinate axis yielded by principal coordinate analysis consistently yielded significant correlations. Such results indicate these data reduction techniques detect differences among the samples in coordinated crown elaboration and simplification. When considered in conjunction with differential tooth size allocation, such results indicate the dentitions of the various samples vary metrically and morphologically independently of antiquity.

Table 15.5. *Straight-line geographic distances between sample pairs among the 18 samples included in both tooth size allocation and dental morphology analyses*

	ChlMRG	CHU	DJR	GPD	HAR	INM	KHO	KUZ	MDK	MOL	NeoMRG	PNT	RAS	SAP	SKH	SWT	TH
CHU	1712																
DJR	860	2460															
GPD	1985	282	2741														
HAR	470	1585	870	1870													
INM	1235	545	2094	814	1188												
KHO	750	1985	400	2267	570	1748											
KUZ	860	2460	0	2741	870	2094	400										
MDK	690	1960	435	2242	535	1723	40	435									
MOL	860	2460	0	2741	870	2094	400	0	435								
NeoMRG	0	1712	890	1985	470	1235	750	890	690	890							
PNT	1985	282	2741	0	1870	814	2267	2741	2242	2741	1985						
RAS	2005	550	2115	804	1208	15	1763	2115	1738	2115	2005	804					
SAP	795	2424	45	2706	830	2064	405	75	412	75	795	2706	2079				
SKH	645	1762	595	2044	345	1533	250	595	220	595	645	2044	1548	580			
SWT	690	1797	590	2050	412	1600	240	590	180	590	690	2050	1615	580	35		
TH	1265	3100	1080	3382	1665	2665	1540	1080	1440	1080	1265	3382	2109	1012	1523	1545	
TMG	425	1818	500	2100	405	1593	185	500	130	500	425	2100	1607	515	110	115	1448

Note: Sample abbreviations are from Table 15.1; distances are in kilometers.

15.4.2 Dental morphology and tooth size: concordant or discordant results?

Does variation in dental morphology yield results consistent with those obtained from allocation of permanent tooth size? A matrix correlation test between the triangular matrix of Smith's MMD values obtained from dental trait frequencies and the triangular matrix of squared Euclidean distances obtained from geometrically scaled mesiodistal and buccolingual diameters found these matrices to be significantly correlated. Further, both matrices were significantly correlated to a triangular matrix of pairwise geographic distances between sample pairs. An examination of the partial correlation of residuals of these two matrices, once the effect of geography was removed, found these residuals to be nonsignificant. Following Oden and Sokal (1992: 289), if a nonsignificant result is obtained by the three matrix permutation test upon two matrices (Smith's MMD values, squared Euclidean distances) that have been demonstrated to be spatially autocorrelated, one can accept the null hypothesis that the two matrices are the product of geographic factors acting upon the same process of differentiation.

Four models were tested to account for patterning in the biological distance matrices. The first assumes that differences between sample pairs are the consequence of the straight-line geographic distances between them (pure autocorrelation). Mantel tests of the relationship between the triangular matrix of Smith's MMD values and the triangular matrix of straight-line geographic distances account for 11.3 percent of the total variation among sample pairs, while a similar test of the relationship between squared Euclidian distances and straight-line geographic distances accounts for 12 percent. A three matrix permutation test with the effect of the reconciled matrix held constant indicates that pure autocorrelation explains little of the patterning ($r = 0.215$; 4.62 percent) behind the shared variation between samples. Such results suggest that while geographic distance plays a role in structuring differences among samples, a model of pure autocorrelation provides a very poor fit. This poor performance is likely a consequence of the strong phenetic differences in dental morphology between the two temporally distinct samples from Mehrgarh and the strong phenetic differences in tooth size between living Khowars from the other two ethnic groups from the Hindu Kush highlands (Swatis, Madaklasht), as well as tribal Chenchus from their Pakanati and Ghompadhompti Hindu caste counterparts in southeast India.

A marked improvement in accounting for the patterning of autocorrelated phenetic affinities is accomplished when samples are differentiated by region. A model based upon bounded sets of *strict regionality* accounts for 45.3 percent of the variation in the autocorrelated phenetic space between samples.

Performance is slightly poorer (44.0 percent) when a porous model allows for stronger similarities among "core" and "peripheral" members of a regional set coupled with weaker similarities between such "peripheral" members and members of other regional sets. By contrast, performance is better (49.1 percent) when such a porous model allows for strong separations within a region between "core" and "peripheral" members coupled with weak separations between "peripheral" regional members and members of other regional groups.

Considered as a whole, analyses based on these two types of data yield some results that are consistent and others that are not. Both identify a core of regional continuity for most regions, and both indicate continuity problems for prehistoric samples from the Indus Valley, especially those that antedate the third millennium BC. The analyses also identify outliers that do not appear to be related to other samples included in this analysis, reveal that samples that combine members of different ethnic groups (castes) are problematic for comparative purposes, and appear unaffected by the inclusion of both prehistoric and living samples. In other cases, the two analyses differ with respect to the phenetic affinities identified for specific samples. Since there is no a priori rationale to favor one system of biological variation over the other, the phenetic affinities for such samples must remain unresolved until further samples are added to the comparative array.

15.4.3 Regional continuity in South Asia or gene flow from outside?

Is the population history of South Asia one of long-standing regional continuity, or has the population of South Asia in general, and of Pakistan in particular, been impacted by significant disturbances of local gene pools by gene flow from populations outside South Asia? Neither morphological nor odontometric data indicate the Bronze Age inhabitants of Tepe Hissar share any biological affinities to either living or prehistoric South Asians. The complete absence of affinities suggests that the numerous parallels in Ghalegay Period IV ceramic wares found in northern Pakistan (Swat) with those recovered from Tepe Hissar detailed by Stacul (1975, 1976) are unlikely to reflect any substantial personal contact between the inhabitants of these two locales. Instead, they may represent chance similarities, similarities due to long-distance trade, or similarities due to common contacts with some other population that served as an intermediary (Antonini 1973).

Both sets of data suggest the inhabitants of Tepe Hissar share some affinities to prehistoric Central Asians, but they differ with regard to the strength of these affinities. Morphological variation indicates moderate affinities, but

the specific sample of Central Asians identified as most proximate phenetically to Tepe Hissar differs. Odontometric data suggest affinities between Tepe Hissar and samples from Central Asia are weak to nonexistent. Intriguingly, the geographically most proximate sample to Tepe Hissar, Altyn depe (ALT), is not only identified as possessing no affinities to other Central Asians, it is also profoundly separated phenetically from the inhabitants of Tepe Hissar. Such results run counter to Masson and Sarianidi's (1972) contention that the close similarities in material culture between Tepe Hissar and Altyn depe suggest that the latter may have been colonized by inhabitants of the former.

If the Aryan Invasion Model is true and populations attributable to the urban centers of Sapalli tepe and Djarkutan (Erdosy 1995; Hiebert 1994, 1998; Hiebert and Lamberg-Karlovsky 1992; Kuzmina 1998; Parpola 1995) crossed the Hindu Kush and emigrated to the Indus Valley during the mid-second millennium BC, then post-Mature Phase inhabitants of the Indus Valley should reflect the biological impact of this invading population. Further, if the distribution of Y-chromosome haplotype R1a reflects the genetic "smoking gun" of these invaders, Indo-Aryan-speaking populations inhabiting much of the northern half of the Indian subcontinent should also reflect the biological signature of these intrusive Central Asians (Bamshad et al. 2001; Mukherjee et al. 2001; S. Roychoudhury et al. 2000; Thanseem et al. 2006; Wells et al. 2001).

None of the results obtained through the analysis of dental morphology or tooth size allocation supports such a scenario. While results obtained from dental morphology provide *some* evidence of less phenetic separation between the latest of the prehistoric Indus Valley samples and the BMAC samples of southern Uzbekistan, this is not evident from either multidimensional scaling or principal coordinates analysis. Similarly, only the plot produced by neighbor-joining cluster analysis shows this phenetic proximity between the BMAC samples and Sarai Khola. Together, these results suggest the material evidence recovered from Quetta (Jarrige and Hassan 1989), Mehrgarh VIII (Santoni 1984), and Swat (Antonini 1973) is unlikely to reflect an actual movement of Central Asians into the northwestern region of South Asia. These results also corroborate a number of recent genetic studies that fail to find any substantial influx of Central Asian genes into South Asian populations (Sahoo et al. 2006; Sharma et al. 2006).

Biological connections between the populations of Central and South Asia appear limited to ethnic groups living in the Hindu Kush highlands of northern Pakistan. Dental morphology suggests these three samples show fairly close affinities to one another. This is especially the case for neighbor-joining cluster analysis and principal coordinates analysis, but is less so for results obtained by multidimensional scaling. Further, dental morphology analyses

yield volatile results with regard to the affinities of these ethnic groups to both living and prehistoric samples from other regions of South and Central Asia. Both neighbor-joining cluster analysis and multidimensional scaling suggest equidistant separations of these Hindu Kush highlanders from southeastern and west-central peninsular Indians, as well as from Mature Phase Harappans and the Late Bronze/Early Iron Age sample from Timargarha, coupled with no affinities to the two temporally distinct samples from Mehrgarh, prehistoric Central Asians, or the Bronze Age inhabitants of Tepe Hissar. By contrast, principal coordinates analysis suggests Hindu Kush highlanders have their closest affinities to peninsular Indians, coupled with no affinities to the prehistoric inhabitants of the Indus Valley, and are especially separated phenetically from prehistoric Central Asians and the prehistoric inhabitants of Tepe Hissar. Odontometric analyses suggest that affinities between these highlanders are not close. Swatis and the inhabitants of Madaklasht are identified as isolates to all other samples, while the Khowar consistently occupy a phenetic position peripheral to prehistoric Central Asians from southern Uzbekistan and the Tedjen Oasis of southeastern Turkmenistan.

Such disparate results may be the consequence of several factors. The first is that these populations, living in remote and extremely challenging environments, may have experienced a series of population bottlenecks and genetic drift. Indeed, such findings were found by Papiha (1996) among groups living in the mountainous sub-Himalayan region of Kinnaur District, Himachal Pradesh. A second possibility is that these groups are marked by such volatility in phenetic affinities because they share little biological affinity to one another or to any of the other samples included in this analysis.

The phenetic affinities of prehistoric samples from the Indus Valley clearly differ between dental morphology and odontometric data sets. Analyses based upon dental traits identify fairly close phenetic affinities among post–fourth millennium BC samples, coupled with a strong phenetic divergence between the two temporally distinct samples from Mehrgarh and these later prehistoric samples. The phenetic divergence of these early samples is so profound that the earlier sample from Mehrgarh stands as an isolate peripheral to living and prehistoric samples from west-central India, while the later sample stands as an isolate peripheral to living samples from southeast India. By contrast, analyses based on tooth size do not confirm the profound phenetic separation between the two samples from Mehrgarh. Although affinities do not appear particularly close, neither sample stands apart as possessing closer affinities to non–Indus Valley samples. Instead, it is the Mature Phase sample from Harappa that has affinities to the west-central peninsular prehistoric sample from Inamgaon. The fairly close phenetic affinities between the two post-Mature Phase samples, Timargarha and Sarai Khola, identified by dental morphology are confirmed by odontometrics.

Such striking differences in the phenetic affinities shown by prehistoric Indus Valley samples that antedate the third millennium BC cannot be attributed to the antiquity of these samples per se, for no correlation was found between tooth size and crown complexity, even though prehistoric samples from South Asia, like those from other world regions, exhibit a tendency toward reduction across the post-Pleistocene era (Lukacs 1985a). The discontinuity in phenetic affinities between prehistoric samples that antedate and postdate the fourth millennium could be interpreted as support for the Early Intrusion Model (Hemphill 1998, 1999; Hemphill et al. 1991, 1998), but this is unlikely.

The affinities identified from dental morphology of the Neolithic inhabitants of Mehrgarh with west-central Indians in general, and with the Jorwe Period inhabitants of Inamgaon, may reflect long-standing population continuity across the subcontinent that dates back to the initial dispersal of humanity to South Asia (Kivisild et al. 2003; McElreavy and Quintana-Murci 2005; Sahoo et al. 2006). Indeed, none of the analyses showed the affinity to be strong. In this regard, it is intriguing that tooth size allocation analysis yields a similar result, except that affinities are limited to the Jorwe Period sample and are closer to the Mature Phase inhabitants of Harappa than to the Neolithic inhabitants of Mehrgarh. Yet, once again, these affinities are not particularly close. Further, it may be that the affinities identified by dental morphology between Neolithic Mehrgarh and Inamgaon and between Harappa and Inamgaon by tooth size may signal patterns of interaction that ceased with the deurbanization of the Indus Civilization near the beginning of the second millennium BC. Neither dental morphology nor tooth size indicates any phenetic proximity between post-Mature Phase Indus Valley samples and peninsular Indians. This lack of relatedness to peninsular Indians extends to living inhabitants of the Hindu Kush highlands as well as to prehistoric Central Asians, while the separation between Indus Valley and peninsular Indians inhabitants has been confirmed for Y-chromosome variations by Sengupta and coworkers (2006; see also McElreavey and Quintana-Murci 2005) and for mtDNA by Quintana-Murci and coworkers (2004; see also Metspalu et al. 2004). Such results run counter to expectations of the Early Intrusion Model. With the "Neolithic Arya" version of Renfrew (1987, 1996) post-Neolithic affinities between Indus Valley samples and peninsular Indian samples make sense, but there is no ostensible reason why such affinities should disappear by the beginning of the second millennium. With the proto-Elamo-Dravidian version, the expected affinities between the Neolithic inhabitants of Mehrgarh and peninsular Indians are unsupported. Thus, this study eliminates the Early Intrusion Model as a viable explanatory theory. Instead, the consistent association of Dravidian-speaking samples with Indo-European-speaking samples from west-central peninsular India suggests a peninsular origin for these groups as well as Dravidian languages (see also Fuller 2003; Sengupta et al. 2006).

When assessing the patterning of affinities possessed by peninsular Indians, dental morphology consistently identifies a regional distinction between ethnic groups from Maharashtra in west-central India relative to ethnic groups from Andhra Pradesh in southeastern India, which corroborates numerous genetic studies consistent with long-standing population continuity and genetic differentiation through isolation by distance (Bamshad et al. 1996; Das et al. 1996; Ghosh et al. 1977; Majumdar 1998; Majumdar and Mukherjee 1993; Majumdar et al. 1999; Metspalu et al. 2004; Sahoo et al. 2006; Sengupta et al. 2006; Walter et al. 1977). However, these results confirm that tribal samples are consistently most distinctive relative to their Hindu caste counterparts, and that the prehistoric sample from Inamgaon is identified as being associated with both living ethnic groups from west-central India as well as prehistoric samples from the Indus Valley. This is consistent with numerous genetic studies that indicate a greater population structuring beyond simple isolation by distance, a structure that distinguishes between tribal and caste Hindu populations (Balakrishnan 1978; Battacharayya et al. 1999; Cordaux et al. 2004; Kivisild et al. 2003; Livshits and Nei 1990; Majumdar 1998; A.K. Roychoudhury 1983). Odontometric analyses likewise consistently identify a regional distinction between living peninsular Indians, but the distinction is not as well marked as that yielded by dental morphology. Results of odontometric analyses tend to identify the tribal samples of each region as divergent. However, odontometric analyses identify the Chenchus of southeastern India as highly divergent from their Hindu caste counterparts, while the Bhils of Gujarat are much less so, a finding that corroborates the assertion of strong genetic differences among tribal populations (Krithika et al. 2009) as well as their differing degrees of genetic separation from caste Hindus due to the absorption of former tribal populations into the caste system through the process of Hinduization (Chaubey et al. 2007).

Analyses of dental morphology and tooth size that include mixed caste urban samples from Kolkata and Pune indicate such samples may be of little utility for elucidating the patterning of affinities among the ethnic groups of South Asia. Both neighbor-joining cluster analysis and multidimensional scaling identified these two samples as showing closest affinities to one another and with secondary affinities to the two Hindu caste samples from southeast India. Principal coordinates analysis identified these two samples bearing affinities to the low-status Hindu caste sample of Gompadhompti Madigas from southeast India. Only the mixed caste urban sample from Pune was included in the tooth size allocation analyses. This sample was not associated with other living samples from west-central India, but was instead peripheral to samples from southeast India. While the results obtained from dental morphology and odontometrics broadly corroborate one another, the affinities of these mixed caste

urban samples to one another and to ethnic groups of southeast India do not make sense linguistically, geographically, or with respect to previous work by others based upon other lines of biological variation. Such results suggest by mixing members of different castes, one is analyzing data that are both socially and biologically meaningless.

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16 *Do all Asians look alike? A dental nonmetric analysis of population diversity at the dawn of the Chinese empire (770 BC–AD 420)*

CHRISTINE LEE AND LINHU ZHANG

16.1 Introduction

Until recently, few nonmetric dental studies have been conducted in Northeast Asia to help unravel population history in the region. Several circumstances have contributed to this situation, including difficulty in traveling to many parts of Asia, limited access to skeletal collections, and a dearth of archaeological reports translated into English. China and Mongolia cover more than 10 million square kilometers and have a combined population of more than 1 billion people. There are at least sixty different ethnicities and three major language families represented within the region (Murphy 1994). The population history of Northeast Asia is long and complicated. Humans have inhabited this area for tens of thousands of years. Agriculture, metallurgy, writing, and long distance trade have existed for more than 4,000 years (Barnes 1999). This chapter discusses how nonmetric dental traits can help clarify how many different populations were present in China and Mongolia in earlier times.

16.2 Previous nonmetric dental trait studies in Northeast Asia

The earliest nonmetric dental trait studies in Asia focused on worldwide migration patterns, often grouping samples from China and Mongolia together. The research of Turner (1987, 1990) on the Asian Sinodont and Sundadont dental complexes did not distinguish among populations within Northeast Asia.

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Modern day Mongolians, Bronze Age Chinese, and modern day southern Chinese all fell within the Sinodont complex. Hanihara's (2008) world study found East/Northeast Asia populations to have the most intraregional variation after sub-Saharan Africa. He concluded that this variability was due to the complicated history of the region with many waves and directions of population movement. Manabe (2003) separated East Asian and North Asian populations to address the origins of the modern Japanese population. East Asians and North Asians clustered together in statistical analyses, but they were still slightly distinct from each other. Matsumura and Hudson (2005) used nonmetric dental traits to detect the origins of Southeast Asian populations. Northern Chinese and southern Chinese samples were close together. The two Chinese and Mongolian samples, however, were slightly divergent. Lee (2007) studied more than 1,000 individuals to determine the synchronic and diachronic movement of people in Northeast Asia from the Neolithic to the present. A distinctive separation was found among populations north and south of the Great Wall. Samples from Mongolia and China were distinct for at least the last 2,000 years.

16.3 The archaeology and history of China and Mongolia

The samples for this study were divided into eight geographical regions based on archaeological cultures (Figure 16.1). These regional divisions appear to have been present from the beginning of the Bronze Age (2000 BCE), and may have extended back to the Neolithic Period (5000 BCE).

16.3.1 Mongolia

The region includes most of the modern day country of Mongolia, except the western border along the Altai and Tianshan mountains. Mongolia is predominantly grassland, with mountains to the north and east, and the Gobi Desert in the south. The long and cold winters last from September to May. Summers are short, hot, and dry (Di Cosmo 2002). While some agriculture was practiced during the Neolithic Period, the main subsistence strategy has been nomadic pastoralism since the Bronze Age. The main types of livestock were horses, cattle, sheep, and goats. Those on the western edge of the region raised camels. Limited agriculture, hunting, and gathering were also practiced (Honeychurch and Amartuvshin 2005). The cultural and political structure in Mongolia has always differed from that of their Chinese neighbors to the south. Culturally, Mongolia has closer connections to Central Asia and southern Siberia. Long

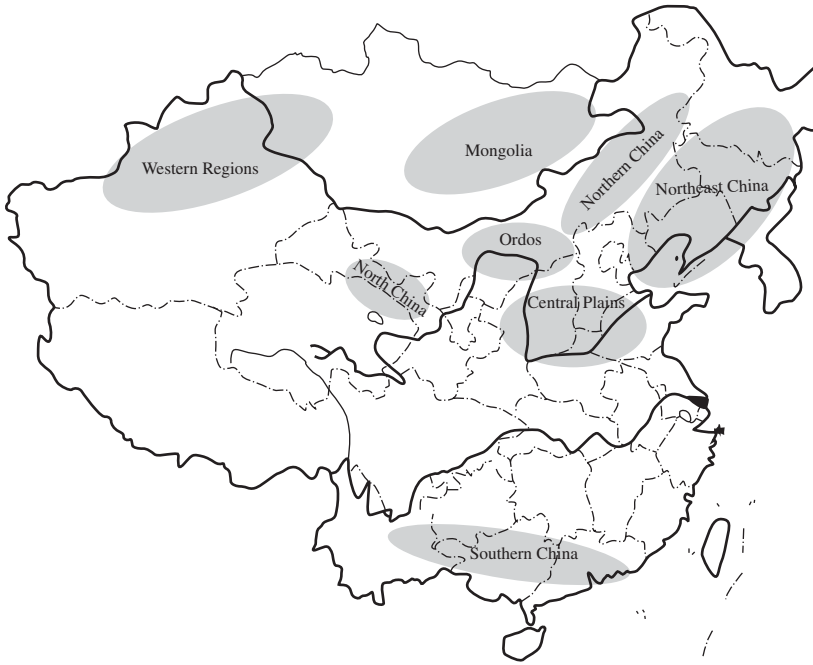

Figure 16.1. Map of the eight study regions.

distance trade networks linked Mongolia to Central Asia and China (Atwood 2004). The main languages spoken in this region belong to the Altaic language family. Turkic, Mongolian, and Manchurian were spoken within the borders of Mongolia throughout the last 2,000 years (Watson 1972).

Archaeological cultures from this region include the Slab Grave (Bronze Age), Xiongnu (Iron Age), and Mongols (Medieval). Craniometric data indicate that this region experienced population continuity since the Bronze Age. There is evidence of some biological admixture from European-derived populations in Central Asia (Chen 2003). Mitochondrial DNA (mtDNA) analysis is also supportive of population continuity for at least 2,000 years (Iron Age) (Keyser-Tracqui et al. 2006). Prior DNA analysis also shows Mongolians are related to European-derived populations in Central Asia and Asians from Siberia (Katoh et al. 2005; Kim et al. 2010). The DNA analysis has detected a severe population bottleneck within the last 1,000 years, probably from the Mongol Conquest (1206–1368) under Genghis Khan (Yao 2002). Mongolians were also found to be divergent from the Chinese. Mongolia is considered the ancestral homeland of modern day Mongolians.

16.3.2 Northern China

Northern China includes present day Inner Mongolia, a portion of eastern Mongolia, and parts of western Manchuria. Populations in this area based their economy on horse and sheep breeding as well as mining iron, copper, silver, gold, and salt. They practiced limited agriculture and had permanent settlements. This is the ancestral homeland of the Xianbei and Qidan people. The Xianbei ruled over portions of Mongolia and China from 93 to 581 CE. The Qidan ruled parts of China and Mongolia from 907 to 1125 CE. Both groups "disappear" as separate peoples by the end of the Mongol Conquest (1368). It is possible they were absorbed by the Jurchens (Manchurians). The inhabitants of this region were part of the Altaic language group, though it is unclear whether they spoke a Mongolian or Manchurian language (Franke 1990; Franke and Twitchett 1994).

On the basis of craniometric data, the Xianbei and Qidan are related to ancient (Xiongnu) and modern day Mongolians (Chen 2003; Zhu 1991). The mtDNA results suggest population interaction in this region with Mongolians (Asian) and Turkic-speaking groups (European-derived) (Fu et al. 2007).

16.3.3 Ordos

The Ordos region is located in the great bend of the Yellow River in Inner Mongolia and Shaanxi Province. It served as a buffer zone between China and Mongolia along the Great Wall. The populations were heterogeneous in both culture and subsistence strategy. Nomadic pastoralists and settled agricultural communities were located in close proximity to each other. They all controlled trade and communication from north to south (Mongolia/China) and east to west (Manchuria/Central Asia). The principal forms of livestock were horse, with some sheep, pigs, and cattle, while the primary crop was millet (Di Cosmo 2002).

16.3.4 Northeast China

This region comprises modern day Manchuria (Heilongjiang Province, Jilin Province, Liaoning Province) and the Korean Peninsula. The western border is a continuation of the Mongolian grasslands. Northeastern China mainly consists of mountains, forests, and rivers. The region's economy was based on millet farming, livestock, hunting, and fishing (Di Cosmo 2002). The archaeological

and historical cultures include the Hongshan (Neolithic), Upper Xiajiadian (Bronze Age), Koguryo (Iron Age), and Jurchen (Medieval). The people of this region are distinctive in their use of burial masks, bear motifs, and dog burials (Di Cosmo 2002; Jin 1987). Traditional languages probably fall within the Tungus (Manchurian) branch of the Altaic family. This region is considered the homeland of Manchurians and Koreans (Barnes 1999; Franke 1990; Murphey 1994); both cultures have had diplomatic relations with Mongolia and China for at least 1,500 years (Byington 2007). Jun et al. (2009) used mtDNA to test the origin of modern Koreans. East Asians separated out by language and geography. Samples from Manchuria and the Korean Peninsula were more closely related to those in Mongolia than to populations in Tibet or China.

16.3.5 Central Plains

The region includes modern Henan, Shanxi, and Shaanxi Provinces along the Yellow River; it is considered the homeland of the Chinese people and civilization. Archaeological cultures include the Yangshao (Neolithic), Zhou (Bronze Age), Zhao (Iron Age), Qin (Iron Age), and Han (Iron Age) (Chang 1986). The main language family is Sino-Tibetan (Chinese) (Norman 1988). Subsistence is primarily based on millet farming and pig husbandry. Permanent settlements with defensive city walls date to the Neolithic Period. The Chinese Empire (206 BCE–220 CE) practiced military expansion and large-scale resettlement of citizens along their frontiers in an attempt to assimilate local populations (Barnes 1999; Bielenstein 1986). The archaeological cultures in this region are distinctive for their sacrificial burials, warfare related decapitations, mass well burials, and evidence of scalping (Chang 1986).

Craniometric studies have shown evidence of Chinese moving into the northern China region (Gu 2007; Jia 2006). Zhu (1994) concluded there was continuity within the Central Plains region from Neolithic to modern times. A nonmetric dental trait study revealed that populations from the Central Plains sample may have interacted with Southern Chinese (Liu and Zeng 1995). The mtDNA analysis suggests that Chinese populations expanded in scope and number within the last 1,000 years, while Mongolians and Tibetans experienced population reduction and genetic drift (Yao 2002).

16.3.6 Southern China

This region includes modern day China south of the Yangzi River. The main languages spoken are in the Sino-Tibetan family, mainly Chinese (Norman

1988). Archaeological cultures include the Dian (Iron Age), Kunming (Iron Age), Ba (Bronze Age), and Shu (Iron Age). Rice cultivation, with pig husbandry and fishing, constituted the local economy. The region is distinguished by its tin and bronze metallurgy, royal burials with sacrificial victims, and cowry shell money. Southern China was incorporated into the Chinese Empire around 100 BCE (Allard 2005; Higham 1996).

16.3.7 Northwest China

Northwest China incorporates Gansu Province and Qinghai Province. Traffic along the Silk Road was controlled by the inhabitants of the region. The main languages spoken fell within the Tibetan branch of the Sino-Tibetan family (Ramsey 1987). Archaeological cultures include the Qijia (Bronze Age), Xindian (Bronze Age), Qiang (Iron Age), and Tangut (Medieval). Material culture is suggestive of cultural continuity from the Neolithic to Medieval Period. Populations had permanent settlements along the Yellow River. Major crops included millet, wheat, and barley. Livestock consisted mainly of horse and pig. Bronze metallurgy and horse breeding made their earliest Northeast Asian appearance in this region. The people of Northwest China have traded with those in the Central Plains and Ordos regions since the Neolithic Period/Bronze Age (Di Cosmo 2002). Burial practices differed from those of the Central Plains region in that children were interred with adults (Higham 1996). Multiple burials within family crypts were common (Qian et al. 2009).

Craniometric traits and mtDNA studies indicate that the archaeological populations are closely related to modern day Tibetans. Genetic data are also indicative of limited admixture from Central Plains groups (Gao et al. 2007; Qin et al. 2010; Zhang 2008; Zhao et al. 2011). This region experienced a population bottleneck around the Medieval Period (Yao 2002).

16.3.8 Western Regions

The final geographic area includes western Mongolia and Xinjiang Province. The geography is stark, with massive mountain ranges (Altai, Tianshan) in the west, and desert basins (Gobi, Tarim, Taklamakan) in the south (Di Cosmo 2002). All European-derived populations in northeastern Asia historically resided within this region. Today this area is inhabited by Altaic language speakers from the Turkic branch, Uighur and Kazak (Ramsey 1987). Indo-European speakers from the Iranian branch were present until the Medieval Period (Mallory and Mair 2000; Watson 1972). Archaeological cultures include

the Afanasievo (Bronze Age), Andronovo (Bronze Age), Scythian (Iron Age), Tarim Basin oasis states (Iron Age), and Uighur (Medieval). The earliest inhabitants were nomadic pastoralists. Their burials were placed under large stone mounds called kurgans, often accompanied by tall stele called deer stones for their deer and sun motifs (Crubezy et al. 1996). The people of this region emigrated from Central Asia in several waves during the Bronze Age (Hemphill and Mallory 2004). Xiongnu, Xianbei, Qidan, and Mongols employed people from this region as administrators within their government; many of the latter eventually settled within Mongolia (Atwood 2004). Ceramics and metalwork suggest technological interaction with northwestern China. Archaeological assemblages in this region indicate close ties to Central Asia and southern Siberia (An 1992). Craniometric and nonmetric dental studies confirm these populations are European-derived. While there is evidence for minimal admixture from Asians, the most likely candidates are Mongolian or northwestern Chinese, not peoples of the Central Plains (Han 2001; Lee 2007; Zhang 2009).

16.4 Materials and methods

Fifty-seven samples from archaeological excavations and medical collections were analyzed for this study (Table 16.1). Data were collected from 1,419 individuals housed at eight institutes in three countries. Most modern samples consisted of dental casts at the School of Human Evolution and Social Change, Arizona State University, Tempe. Archaeological skeletal data were recorded at the National University of Mongolia (Ulaan Baatar, Mongolia), National Museum of Mongolia (Ulaan Baatar, Mongolia), Henan Province Archaeological Institute (Zhengzhou, China), Yunnan Province Archaeological Institute (Kunming, China), Gansu Province Archaeological Institute (Lanzhou, China), the Institute of Vertebrate Paleontology and Paleoanthropology (Beijing, China), and the Center for Chinese Frontier Archaeology, Jilin University (Changchun, China). All data were recorded by the first author.

The Arizona State University Dental Anthropology System (ASUDAS) was used to score nonmetric dental traits (Turner et al. 1991). Up to twenty-six maxillary and mandibular morphological traits were scored for each individual with permanent teeth. Dental traits were selected to distinguish best among Northeast Asian samples. Data from each individual were scored for trait presence or absence based on standard breakpoints (Table 16.2). The percent present for each was calculated by sample. The average percentages were then totaled within each of the eight regions.

Table 16.1. *The eight study sites*

Sample	N	Period	Provenance	Institution	Reference
Mongolia					
Slab Grave	5	Bronze Age	Eastern Mongolia	NUM	(Erdenebaatar 2002)
Xiongnu	62	Iron Age	Mongolia	NUM, NMM	(Torbat 2004)
Mongol	41	Medieval	Mongolia	NUM, NMM	
Mongolian	4	Modern	Mongolia	NUM	
Total	112				
Northern China					
Zhaizitai	8	Bronze Age	Inner Mongolia	Jilin	
Dongdajing	10	Iron Age	Inner Mongolia	Jilin	(Inner Mongolia Archaeological Institute 2004)
Huhewusu	7	Iron Age	Inner Mongolia	Jilin	(Inner Mongolia Archaeological Institute 2004)
Zhalainuoer	6	Iron Age	Inner Mongolia	Jilin	(Inner Mongolia Cultural Relics Bureau 1961)
Sandaowan	8	Iron Age	Inner Mongolia	Jilin	(Inner Mongolia Archaeological Institute 2004)
Lamadong	37	Iron Age	Liaoning	Jilin	
Chengpuzi	11	Medieval	Inner Mongolia	Jilin	
Beiwei	10	Iron Age	Shanxi	IVPP	(Shanxi University, Shanxi Province Archaeological Institute, and Datong Museum 2006)
Shanzuizi	15	Medieval	Inner Mongolia	Jilin	(Zhu 1991)
Total	112				
Northwestern China					
Donghuishan	12	Bronze Age	Gansu	Jilin	(Gansu Province Archaeological Institute and Jilin University 1998)
Xiaohandi	5	Bronze Age	Qinghai	Jilin	(Qinghai Cultural Relics Bureau 1995)
Mapai	5	Bronze Age	Qinghai	Jilin	
Mogou	81	Bronze Age	Gansu	GIA	(Gansu Province Archaeological Institute and Xibei University 2009)
Taojiazhai	110	Iron Age	Qinghai	Jilin	(Qinghai Province Archaeological Institute 2007)
Total	213				

(*continued*)

Table 16.1. (*cont.*)

Sample	N	Period	Provenance	Institution	Reference
Northeastern China					
Guanmashan	12	Bronze Age	Jilin	Jilin	(Jilin Province Archaeological Institute 1991)
Shiertai	7	Bronze Age	Liaoning	Jilin	(Zhu 1960)
Longtoushan	9	Bronze Age	Inner Mongolia	Jilin	(Qi 1991)
Pinganpu	8	Bronze Age	Liaoning	Jilin	(Liaoning Province Archaeology Institute 1989)
Wanfabozi	16	Iron Age	Jilin	Jilin	(Jin 2001)
Shitaizi	9	Iron Age	Liaoning	Jilin	(Liaoning Province Archaeological Institute and Shengyang City Archaeological Institute 2008)
Dashanqian	4	Iron Age	Inner Mongolia	Jilin	(Zhu et al. 1998)
Shuiquan	14	Iron Age	Inner Mongolia	Jilin	(Inner Mongolia Archaeology Institute 2005)
Huangyuquan	2	Medieval	Jilin	Jilin	
Korean	16	Modern	United States	ASU	
Total	97				
Ordos					
Zhaimao	22	Bronze Age	Shaanxi	Jilin	(Shanxi Province Archaeological Institute 2002)
Xicha	4	Bronze Age	Inner Mongolia	Jilin	(Inner Mongolia Archaeology Institute 2001)
Ximaqing	14	Iron Age	Inner Mongolia	Jilin	
Guoxianyaozi	3	Iron Age	Inner Mongolia	Jilin	(Inner Mongolia Archaeology Institute 1989)
Yinniugou	11	Iron Age	Inner Mongolia	Jilin	(Inner Mongolia Archaeology Institute and Kyoto University 2001)
Shuangqucheng	7	Iron Age	Inner Mongolia	Jilin	(Inner Mongolia Archaeology Institute 2009)
Total	61				
Central Plains					
Miaozigou	8	Neolithic	Inner Mongolia	Jilin	(Inner Mongolia Archaeological Institute 2003)
Mianchi Duzhong	16	Neolithic	Henan	HIA	(Sun 2007)
Xiawanggang	70	Neolithic	Henan	IVPP	(Henan Archaeology Institute 1989)
Youyao	20	Bronze Age	Shanxi	Jilin	(Xinzhou City Archaeological Institute 1989)

Xishuipo	30	Bronze Age	Henan	Jilin	(Puyang City Archaeological Institute 1989)
Wadian	4	Bronze Age	Henan	Jilin	(Henan Province Archaeological Institute 2004)
Yujiawan	23	Bronze Age	Gansu	Jilin	(Gansu Province Archaeological Institute 2009)
Neiyangyuan	44	Iron Age	Shanxi	Jilin	
Tuchengzi	64	Iron Age	Inner Mongolia	Jilin	(Inner Mongolia Archaeological Institute 1991)
Xuecun	90	Iron Age	Henan	HIA	(Henan Province Archaeological Institute 2007)
Longxian	45	Iron Age	Shaanxi	IVPP	(Shanxi Province Archaeological Institute 1998)
Huabei	107	Modern	Hebei	IVPP	
Total	521				
Southern China					
Jinlianshan	123	Iron Age	Yunnan	YIA	(Yunnan Province Archaeological Institute, Yuxi Cultural Relics Bureau, Chengjiang Cultural Relics Bureau, and Jilin University 2011)
Yunnan	78	Modern	Yunnan	IVPP	
Cantonese	74	Modern	United States	ASU	
Taiwanese	23	Modern	United States	ASU	
Total	298				
Western Regions					
Khrigsur	9	Bronze Age	Western Mongolia	NUM, MNN	
Nileke	19	Iron Age	Xinjiang	Jilin	(Xinjiang Province Archaeological Institute 2002)
Yanghai	64	Iron Age	Xinjiang	Jilin	(Xinjiang Turfan Research Institute and Xinjiang Province Archaeological Institute 2011)
Yingpan	23	Iron Age	Xinjiang	Jilin	(Xinjiang Province Archaeological Institute 2001)
Jilinatai	60	Iron Age	Xinjiang	Jilin	(Ruan 2004)
Chandman	40	Iron Age	Uvs	NUM	(Tsevendorj 2007)
Uighur	3	Medieval	Ovorkhangai	NMM	
Total	218				
Total	1,419				

NUM – National University of Mongolia, NMM – National Museum of Mongolia, Jilin – Jilin University, ASU – Arizona State University, IVPP – Institute of Vertebrate Paleontology and Paleoanthropology, HIA – Henan Province Archaeological Institute, GIA – Gansu Province Archaeological Institute.

Table 16.2. *Nonmetric dental trait percentages*

		Western Regions	Mongolia	Ordos	N. China	NE China	Central Plains	S. China	NW China
Dental trait	Breakpoint	%	%	%	%	%	%	%	%
Winging I1	1	11	9	20	30	14	5	8	15
Shoveling I1	3–6	19	31	53	29	59	79	55	92
Double shoveling I1	2–6	24	41	8	56	60	73	49	88
Interruption groove I2	1	34	30	10	21	21	35	32	14
Tuberculum dentale I2	1–6	17	10	12	4	16	5	16	0
Hypocone M2	0–1	33	21	8	20	5	16	24	11
Cusp 5 M1	1–5	4	10	8	8	6	3	11	7
Carabelli's cusp M1	2–7	19	19	9	12	18	17	17	16
Parastyle M3	1–5	3	3	0	3	0	2	5	0
Enamel extension M1	1–3	20	30	28	43	46	46	41	33
Root number M2	3	72	62	76	58	62	74	52	60
Root number PM1	2	51	33	40	29	22	24	28	23
Peg/absence M3	1–2	68	51	58	50	35	49	45	49
Cusp number PM1	2–9	17	29	15	11	13	18	30	21
Cusp number PM2	2–9	69	56	76	80	68	72	85	67
Y-groove M2	Y	36	32	24	15	37	23	48	16
Cusp number M1	6	5	9	3	3	9	10	11	19
Cusp number M2	4	81	67	66	60	63	62	50	46
Deflecting wrinkle	3	10	21	8	4	16	28	40	24
Protostylid M1	2–7	1	3	19	5	29	11	27	28
Cusp 6	1–5	5	9	4	7	10	12	12	16
Cusp 7	1–5	8	4	2	5	0	4	5	1
Root number M1	3	1	7	28	12	32	17	14	27
Root number M2	1	17	29	44	52	46	43	27	36
Root number PM1	2	2	1	0	0	2	2	4	1
Root number PM2	2	0	0	0	0	0	0	0	0

Table 16.3. *Mean measure of divergence results over standard deviations*

	Mongolia	N. China	NW. China	NE. China	Ordos	C. Plains	S. China	W. Regions
Mongolia	0	.0290	.1715	.0625	.0472	.0739	.0483	.0299
Northern China	.0124	0	.1522	.0551	.0300	.0884	.1040	.0928
Northwestern China	.0080	.0106	0	.0647	.1760	.0501	.1307	.3610
Northeastern China	.0111	.0134	.0091	0	.0367	.0348	.0435	.2014
Ordos	.0176	.0199	.0158	.0189	0	.1110	.0923	.0960
Central Plains	.0061	.0087	.0042	.0073	.0139	0	.0662	.1999
Southern China	.0071	.0095	.0051	.0083	.0148	.0032	0	.1575
Western Regions	.0081	.0108	.0062	.0092	.0158	.0043	.0052	0

16.5 Results and discussion

Based on averaged population percentages for the eight regions, eight traits were key in distinguishing samples: UI1 shoveling, UM2 hypocone absence, UP1 2-roots, LM1 deflecting wrinkle, LM1 protostylid, LM1 cusp 6, LM1 three-roots, and LM2 one-root. The following traits distinguished between Central Asian (European-derived) and Asian populations: UI1 winging, UI1 shoveling, UI1 double shoveling, UI2 tuberculum dentale, UM2 hypocone absence, M3 congenital absence, LM1 cusp number, LM2 cusp number, LM1 deflecting wrinkle, LM1 protostylid, LM1 three-roots, and LM2 one-root.

The mean measure of divergence (MMD) statistic was used to estimate intersample phenetic distances (Table 16.3) (Sjøvold 1977). The MMD result is statistically significant if it is larger than two times the standard deviation (Sjøvold 1973). All resulting distances are statistically significant except for two comparisons. The Ordos sample is not distinct from those of northern China and northeastern China. The Ordos, northern China, and northeastern China samples probably share a common ancestor. The most distinct samples were the Western Regions and northwestern China. These two are the most geographically isolated, providing some barriers to outside interaction. The northwestern population was distinct from its geographic neighbors. Northwest China had some interaction with the Central Plains region. The Western Regions exhibit the highest MMD scores, implying no significant population admixture between the populations of this and other regions. The Western Regions had minimal interaction with Mongolia. According to the

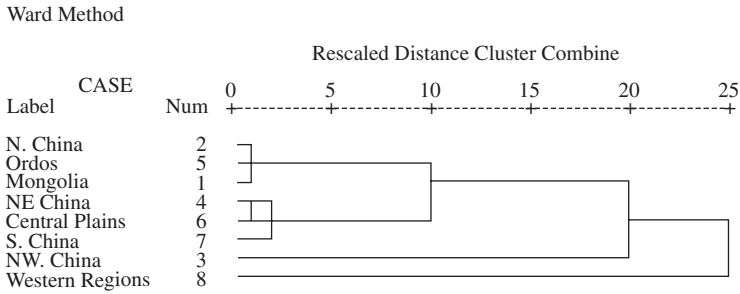

Figure 16.2. Cluster analysis of MMD distances among the eight regional samples.

MMD results, there are seven distinct populations within Northeast Asia. The Ordos sample is probably not a distinct population, but a subset of either northern China or northeastern China.

The distance matrix was subjected to cluster analysis using Ward's algorithm to help visualize relationships (Figure 16.2). The eight regional samples divide into four distinct groups. Northwest China and the Western Regions form two distinct clusters. Northern China, Ordos, and Mongolia form the third group. These samples probably represent areas that were politically allied to the Mongolian Empire. Northeastern China, Central Plains, and Southern China form the last cluster. These latter samples may have been politically allied with the Chinese Empire. These four groups are likely representative of the political situation up to the Medieval Period, because the majority of samples date before this time.

To visualize potential relationships further, distance values were analyzed through multidimensional scaling (MDS) (Figure 16.3). Ordos and northern China are close to one another, suggesting they may be one homogeneous population. Northeastern China, Central Plains, and Southern China form one group, while northern China, Ordos, and Mongolia form another. This result parallels and confirms the cluster analysis. However, with MDS, the positions of northwestern China and the Western Regions become more evident. Northwestern China is still distinct from the other samples but is somewhat closer to Central Plains (Chinese). The Western Regions, on the other hand, is closer to Mongolia. In essence there are two macrogroups, one centered in China and another in Mongolia.

16.6 Summary and conclusions

Nonmetric dental traits were used to gain insight into the population history of northeastern Asia. More than 1,000 individuals were divided into eight

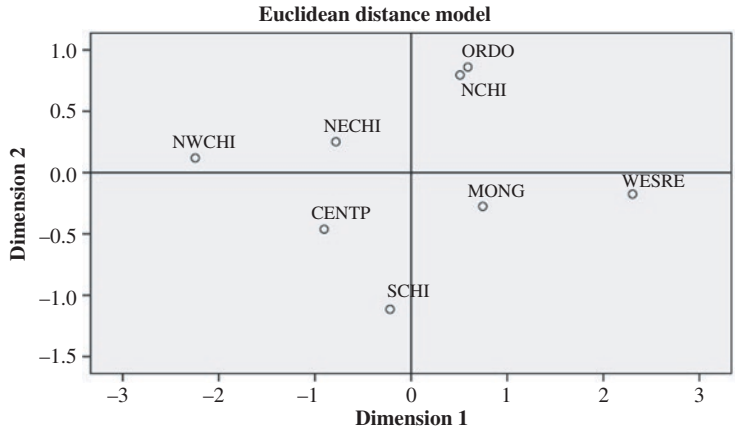

Figure 16.3. Two-dimensional multidimensional scaling of MMD distances among the eight regional samples.

geographic samples based on archaeological culture and historical records. At least one, Ordos, was likely not a distinct population. It probably represents the westernmost extension of the northern China region. The remaining seven samples may represent potentially distinct populations. This finding suggests there were at least seven geographically restricted areas, inhabited by groups that did not often exchange genes with neighboring peoples.

Two main interaction spheres were discovered in Asia. The first encompasses samples allied historically with the Chinese Empire (northeastern China, Central Plains, Southern China, and northwestern China). The Central Plains represents not only the governmental center of the Chinese Empire but the region of origin for the Chinese ethnically. Most samples in this cluster were sedentary agriculturalists who spoke a Sino-Tibetan language. The only exception is the northeastern Chinese, who speak an Altaic language, that is, Manchurian. However, the last dynasty in China was ruled by Manchurians and it is probable that they adopted the Chinese language during their rule.

The second main division encompasses populations allied historically with Mongols (Mongolia, northern China, Ordos, and the Western Regions). The primary means of subsistence for groups in this region was nomadic pastoralism, and they predominantly spoke an Altaic language. Mongolia appears to be the center of this group, possibly because it is the homeland of modern Mongolians.

While the Western Regions and northwestern China had some interaction with the Central Plains and Mongolia, they still appear to be distinct populations. Both regions were independent countries before the Mongol Conquest

(1206–1368). The Western Regions is the most isolated area in this study, geographically and biologically. Thus, the outcome is predictable as this region contains European-derived populations. The slight interaction with Mongolians echoes historical, craniometric, and DNA studies that all indicate some admixture. The inhabitants of the northwestern China region show some biological interaction with those in the Central Plains. Such interaction may be an artifact of their control of the Silk Road.

In sum, this study was undertaken to demonstrate the complexity of the population structure in Northeast Asia. Seven separate populations were detected within Northeast Asia. In essence, the Great Wall apparently proved to be a biological division for thousands of years. It basically serves as a physical (China/Mongolia), cultural (nomadic pastoralism/agricultural), linguistic (Altaic/Sino-Tibetan), and mental divide. Only geographic differences have been investigated here. Future studies will focus on changes and reversals of population movement through time.

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17 *Sinodonty and beyond: hemispheric, regional, and intracemetery approaches to studying dental morphological variation in the New World*

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17.1 Introduction

The development of dental morphology as a human science (see review in Scott and Turner 2006) was a decidedly "Indian"-centric undertaking from the beginning. In fact, there are few better-known anthropological facts that make their way into public consciousness (through forensic sciences TV shows) than the association between Native Americans and shovel-shaped incisors. Whether because of actual evolutionary relevance, historical precedence, or utilitarian ease, shoveling has become one of the most recognized signatures of Native American ancestry. Supplemented but not supplanted, decades of research by dozens of scholars have expanded our view of Native American dental morphology and what it means about the evolutionary history of New World populations. Without a doubt, Turner (1969, 1971, 1981, 1983a, b, 1984, 1985a, b, 1986a, 1987, 1990a, 1991, 1992a, 1993, 1994, 2002, 2006; Turner et al. 1991; Turner and Scott 2007) and his students (Haeussler and Turner 1992; Lee and Scott 2011; Scott 1980, 1992, 2008; Scott et al. 1983, 1988; Scott and Turner 1988, 1997, 2006) have advanced the study of Native American dentition most significantly over the last four decades, work that has been subject to recent and thorough review (Scott and Turner 1997, 2006; Turner and Scott 2007). Our goal here is not to rehash those syntheses or

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add a new angle of historical relevance. Rather, we reaffirm the unique relevance of dental anthropology to variously scaled loci of study, ranging from peopling of the Americas to other topics typically approached in a more contextual fashion in bioarchaeology such as ritual violence, kinship analysis, and ethnogenesis. As such, this review reflects the multidimensional nature of dental morphological research, reasserting the value of dental morphology for reconstructing the origins, migrations, lifestyles, and mortuary practices of indigenous Americans.

17.2 Global and continental perspectives on Native American dental morphology

World geography allows clear delineation of New World dental morphology at the global level. Such efforts began with Hrdlička (1920) and were expanded by Dahlberg (1945, 1951, 1959, 1968) and Pedersen (1949) and subsequently by Hanihara (1968), Turner (1983a, 1990) and many others (see historical overview in Scott and Turner 2006). Here we summarize the most recent and comprehensive assessments – Hanihara (2008) is most regionally comprehensive while Scott and Turner (1997) present the most inclusive list of trait frequencies.

Hanihara (2008) constructed a global database including 12 New World regional aggregates representing 1,045 individuals examined for 15 dental morphological traits (see table 1 in that publication). In comparison to the global average, North and South American Indian populations demonstrated higher frequencies of UI1 and UI2 shoveling, UI1 double shoveling, LP1 central ridge, LM1 cusp 6, LM1 deflecting wrinkle, and LM2 cusp 6. Traits that were on average lower in frequency in comparison to the global sample included UP2 premolar accessory cusps, UM1 Carabelli's cusp, LM1 cusp 7, and LM2 grade 2+ (hypoconulid present). Native American populations were about average in terms of the frequency of UP1 premolar accessory cusps, UM2 grade 3+ (hypocone present), LM1 protostylid, and LM1 distal trigonid crest. Within the New World, South American Indians demonstrated lower intraregional diversity, suggesting a bottleneck at Mesoamerica or serial founder effects during the southward migration of Amerindian populations during the initial colonization of the continent. This finding is consistent with recent genetic surveys (Bisso-Machado et al. 2011; Estrada-Mena et al. 2010; González-José and Bortolini 2011; Hunley and Healy 2011; Lewis 2010; O'Rourke 2011), though not all craniometric analyses have supported the idea of a bottleneck (González-José and Bortolini 2011). In addition, the South American sample demonstrated lower frequencies of UI2 shoveling, UI1 double shoveling, LP1 central ridge, LM1 cusp 6, LM1 deflecting wrinkle, and LM2 cusp 6 in

comparison to the North American sample, although we are unsure whether the differences are statistically significant.[1]

Scott and Turner (1997) summarized world variation for 23 dental traits, dividing New World variation into three divisions (North and South America, Northwest North America, American Arctic) coinciding with the tripartite model of Greenberg, Turner, and Zegura (1986; Scott and Turner 2006; Turner and Scott 2007). Native Americans in their dental morphology demonstrated "greater morphological elaboration than populations from any other geographic area" (Scott and Turner 1997:236) and at the same time were relatively homogenous inter- and intraregionally within the Western Hemisphere (Turner 1983a). Scott and Turner (1997) identified eight high frequency traits (with respect to the global average) that characterized New World populations: winging, shoveling, double shoveling, and interruption grooves on the incisors; premolar odontomes; and molar enamel extensions, LM1 cusp 6, and LM1 deflecting wrinkles (Figure 17.1). This list is nearly identical to that of Hanihara (2008). Maxillary premolars and molars show a tendency toward being single rooted while three-rooted mandibular first molars are found at an unusually high frequency. Other recognized morphological variants of the dentition either are relatively rare in New World populations or are about average with respect to global frequency (see Scott and Turner 1997:237).

Although Turner's work (1967, 1969, 1971, 1976, 1981, 1983a, b, 1984, 1985a, b, 1986a, b, 1987, 1989, 1990a, b, 1991, 1992a, b, c, d, 1993, 1994, 1995, 2002, 2006; Turner and Bird 1981; Turner and Hanihara 1977; Turner and Lien 1984; Turner and Markowitz 1990; Turner and Scott 1977, 2007) and the ASUDAS (Turner et al. 1991), which developed in concert, focus on polymorphic dental variation, other crown and root traits should also be acknowledged. These variants are generally rare and often of clinical interest. Dental anthropologists and clinicians tend to treat these features as anomalies and their geographic patterning is usually not of concern. However, casual perusal of commonly used trait lists indicates the dividing line between polymorphism and anomaly can be arbitrary; odontomes and distosagittal ridges are included in the ASUDAS while talon cusps, incisor twinning, dens in dente, and tooth rotations (as opposed to incisor winging), in addition to a suite of root and crown variants associated with Alt's work (Alt 1991; Alt and Vach 1998), are not.[2] We

[1] Scott and Turner (2006) present frequencies for UI1 double shoveling and LM1 cusp 6 that do not show the same pattern differences between North and South American samples. The difference documented in Hanihara (2008) is likely not statistically significant.

[2] This is not the place to review the history of the ASUDAS and consider how specific traits were chosen or excluded from the final listing (the senior editor is in a better position to write that chapter). We do note, however, that new traits are being identified (Burnett et al., 2010; Weets 2009) and these efforts may help define new directions in New World dental morphological research.

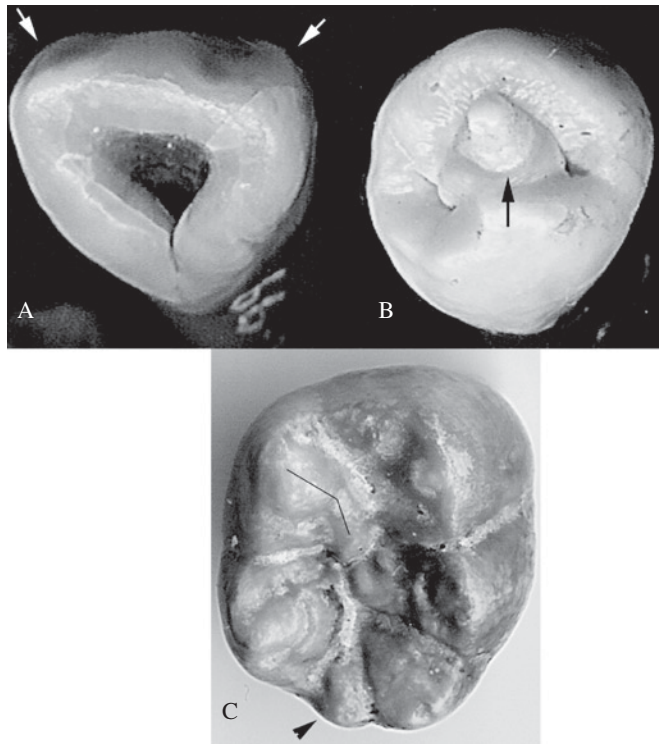

Figure 17.1. Key morphological features of the Native American dentition. A. Extreme shoveling and double shoveling (white arrows) in a maxillary incisor. B. Mandibular premolar odontome. C. Lower left first molar with cusp 6 and deflecting wrinkle. (Please see color plate section.)

mention this here only to emphasize that the preceding characterization of New World dentition includes a subset of the recognized morphological variation; systematic global surveys of rare morphological variants are extremely uncommon. However, understanding the global distribution of rare traits has potential clinical relevance (for example, C-shaped root configurations in endodontics), forensic applications (in terms of individuation [Edgar 2005, 2009; Willermet and Edgar 2009]), and bioarchaeological relevance with respect to kinship analysis (Alt and Vach 1998; Stojanowski and Schillaci 2006). In addition, from rare features one may infer population history, structure, and demography. For example, the work of Powell (1995, 2005) and Stojanowski and Johnson (Johnson et al. 2011; Stojanowski et al. 2011) demonstrates that talon cusps, premolar distosagittal ridges, and dental malpositionings were fairly common in southeastern U.S. Archaic populations. Such traits could reflect a recent

bottleneck coincident with the initial peopling of the Americas or some aspect of group structure as populations expanded throughout the continent.[3] Thus, rare dental traits may be analogous to private alleles that have recently proven useful in discerning the pattern of Native American genetic variability at a finer scale of resolution (Battilana et al. 2006, 2007; Estrada-Mena et al. 2010; Kashani et al. 2011; Lell et al. 2002; Perego et al. 2009; Schroeder et al. 2007, 2009; Schurr 2004; Starikovskaya et al. 2005; Wang et al. 2007).

Patterns of variation *within* the New World are also relevant for inferring evolutionary history. Hanihara (2008) does not discuss spatial variation and most regional research programs (e.g., Griffin 1993; Griffin et al. 2001; Sutter 1997, 2000, 2005a, b, 2009a, b; Sutter and Sharratt 2010) and certainly intrasite or intracemetery studies (Stojanowski and Schillaci 2006 for review; see later discussion) are less concerned with broad geographical comparisons within a racial or geographic framework. Turner's work (1983a, 1984, 1985a, b, 1986a, 1992a, 2002), summarized most recently by Turner and Scott (2007), identifies relatively low variation among Macro-Indian/Amerind populations, no evidence for clinal variation from north to south, no evidence for significant geographic clustering of populations, regional continuity between the earliest and latest populations within a region, no bottleneck through Mesoamerica (contra Hanihara 2008), and no significant differences between North and South American Native American populations in terms of trait frequencies.

However, these observations focus exclusively on the presumed earliest Macro-Indian migratory wave associated with the Clovis/pre-Clovis Paleoindian migration. Turner's classic reading of the *overall* spatial dimension of dental morphology invokes the tripartite model linking linguistic, (then) genetic, and dental data in a cohesive interpretive framework (Greenberg et al. 1986). Here, an initial wave of migrants crossed Beringia and gave rise to all subarctic North and South American Amerindians; a second wave composed of speakers of the Na-Dené/Athapaskan language family settled in the Pacific Northwest, parts of western Canada and Alaska, and eventually parts of the desert U.S. Southwest; and a third wave composed of the arctic adapted Eskimo-Aleut populations of Alaska and Canada (Scott and Turner 1997; Turner 1983a, 1984, 1985a, b, 1986a, 1992a, 2002; Turner and Scott 2007).

Differentiation of these three waves was initially based on frequencies of a single trait (three-rooted LM1 – Turner 1971) but has since expanded to include a larger list that generally places the Na-Dené populations at an intermediate

[3] According to Powell (2005:234; see also Powell 1995), Paleoindians also "express rare and unique traits, and a high degree of dental developmental problems typical of the effects of genetic drift and/or inbreeding." Other authors have documented dental anomalies in Paleoindian remains. For example, the Midland skeleton (Stewart 1955) and Horn Shelter No. 1 (Young 1988) from Texas exhibit ectopic (nasal) teeth.

trait frequency to the Amerind and Eskimo-Aleut samples (Turner 1983a, 1985a, b, 1986a, b, 1992a, 1994; Scott and Turner 2008). The evolutionary significance of the intermediate trait frequencies has been a long-standing concern of Turner's research (Scott and Turner 2008; see also Powell 1993, 2005). The most recent syntheses avoid using the Na-Dené label and differentiate Aleut-Eskimos from "northern United States and Canadian groups, including, but not restricted to, putative Na-Dené-speaking populations (Athapaskan-Eyak, Tlingit, and Haida)" from "southern Indians," the latter encompassing the Amerind/Macro-Indian division (Scott and Turner 2006:659).

Therefore, intracontinental variation was largely explained by three waves of migrants emigrating from three distinct regions of northeast Asia, followed by rapid colonization of North and South America by the earliest group (Amerinds) with relatively minor regional differentiation occurring over a relatively short period and reflecting the action of genetic drift. Importantly, all three proposed founding populations are variants of the Sinodont dental pattern found throughout the Americas and northeast Asia; this observation, combined with the tripartite division just described, flavored Turner's overall interpretation of circum-Pacific population history (Turner 1967, 1969, 1971, 1976, 1983a, b, 1984, 1985a, b, 1986a, b, 1987, 1989, 1990a, b, 1991, 1992a, b, c, d, 1993, 1994, 1995, 2002; Turner and Bird 1981; Turner and Hanihara 1977; Turner and Lien 1984; Turner and Scott 1977, 2007), a topic we turn to next.

17.3 On Sinodonts, Sundadonts, and the peopling of the Americas

Shovel shaped incisors were the initial link between New World and East Asian populations (Hrdlička 1920). Hanihara (1968) expanded the definition of "Mongoloid" dentition to include high frequencies of incisor shoveling, LM1 cusp 6, and deflecting wrinkle. Subsequently, Turner (1983b, 1990a, 2006) subdivided the basic Mongoloid dental complex into two regional variants based on observations of thousands of dentitions from the Pacific Rim. So-called Sundadonts were found in southeast Asia and reflected a less specialized and less elaborated (ancestral) dentition (while still considered classically Mongoloid). Sinodonts were found in northeast Asia and the New World and reflected a specialized dentition that elaborated eight key crown and root features.[4] Presumably Sinodonty evolved from Sundadonty through

[4] These features are now well known and include higher frequencies of three-rooted LM1, LM1 deflecting wrinkle, peg-shaped or absent UM3, UM1 enamel extensions, one-rooted UP1, and UI1 shoveling and double shoveling. Sinodonts also exhibit lower frequencies of four-cusped LM2 in comparison to Sundadonts.

genetic isolation by at least 20 kya. This population subsequently expanded throughout northeast Asia and Siberia where microdifferentiation occurred, thus establishing sufficient dental variation in the Old World to explain New World variability with respect to the three stages of migration in the tripartite model. It is important to note that Sinodonty and Sundadonty are not defined on the basis of the presence of different morphological features, but rather in terms of the frequency of key features and for some traits (such as shoveling) the intensity of expression (Turner 1990a). This latter fact, apparently, allows allocation of individual dentitions to either category, but these statements are often decoupled from formal statistical testing. By the early 1990s Turner's large database and seeming clarity of pattern, combined with the interdisciplinary appeal of the tripartite model, established the standard paradigm of the day (Bolnick et al. 2004; Estrada-Mena et al. 2010; Mazières 2011; Ray et al. 2010; Schurr 2008).

However, the field as a whole is currently undecided about the tripartite model's contemporary utility. While it is mentioned as a historical footnote in several recent genetic studies (de Azevedo et al. 2011; Estrada-Mena et al. 2010; O'Rourke and Raff 2010; Perego et al. 2009; Ray et al. 2010), few actually anchor their research with the model serving as the null hypothesis (cf. Arnaiz-Villena et al. 2010; Schroeder et al. 2007). In fact, many do not reference the tripartite model at all (Kashani et al. 2011; Kemp and Schurr 2010; Lewis 2010; Manríquez et al. 2011; O'Rourke 2011; Perego et al. 2010; Raff et al. 2011; Rubicz et al. 2010). Recent genetic literature fails to support the model's migration scenario (cf. Reich et al. 2011); instead, one of the following scenarios is favored: (1) a single origin from an Asian source isolated in Beringia prior to colonization of the Americas (Estrada-Mena et al. 2010; Fagundes et al. 2008; Kitchen et al. 2008; Mulligan et al. 2008; Schroeder et al. 2007, 2009; Tamm et al. 2007; Wang et al. 2007); (2) a dual origin (Gilbert et al. 2008; Rasmussen et al. 2010); or (3) more complex possibilities involving one or more migrations from a single heterogeneous source – perhaps via different migration routes – followed by recurring, bidirectional gene flow between the Americas and Asia for several thousand years (Kumar et al. 2011; O'Rourke and Raff 2010; Perego et al. 2009, 2010; Ray et al. 2010; Rubicz et al. 2010; Tamm et al. 2007; see also González-José and Bortolini 2011; Mazières 2011).[5]

Recent craniometric studies also largely avoid explicit testing of the tripartite model. Specifically the discovery of, and debacle surrounding, Kennewick Man's supposed Caucasoid features (Chatters 2000, Chatters et al. 1999)

[5] Molecular data do not allow us to differentiate between a single migration and several migrations from the same source population (Arnaiz-Villena et al. 2010; O'Rourke 2011).

and the (re)recognition that early Paleoindian skulls (particularly in South America and Mexico) aligned with populations from Melanesia and Africa (see Anderson 2010:320–321; Fiedel 2000:62; Mazières 2011:499; Neves and Blum 2000; Neves et al. 2004:494 for review; Neves et al. 1996; 1999a, b; 2001, 2003, 2007b; Neves and Hubbe 2005; Neves and Pucciarelli 1989, 1991; Powell and Neves 1999; Powell and Steele 1992) established doubts about the homogeneity and affinity of early American remains; thus the homogeneity implied by the pan-Sinodont and Clovis first models was contradicted.

While details of the tripartite model were being challenged by new and accumulating archaeological, genetic, and craniometric evidence, challenges to the pan-Sinodont model occurred from within dental anthropology. Powell (1993) published a methodological critique of Turner's work, noting issues with sample size variation, regional and temporal pooling of samples, use of the MMD statistic, assumption of equal evolutionary rates of divergence, and Paleoindian sample composition (see later discussion). Yet, despite using more formal cladistic approaches, Powell (1993) basically verified the central tenets of the tripartite model. A key observation was that the small Paleoindian sample consistently held a distinct, basal position that added to the burgeoning evidence that the earliest Native Americans were phenotypically distinct from near-modern samples composing most of Turner's database. Given the time separating modern and Paleoindian samples, such distinction should come as no surprise. Powell's dismissal of Turner's research (despite supporting the conclusions in the end) established a confrontational tone that has not abated. Camps developed, and a certain recalcitrance characterized subsequent literature such that basic agreement over the same dentitions was often contentious. Powell's later work (1995, 1997, 2005; Powell and Neves 1998), however, as well as that of Sutter (1997, 2000, 2005b, 2009b), attempted to move beyond the pan-Sinodont model, but with only limited impact as judged by citation practices in recent syntheses of the peopling of the Americas literature (see Dillehay 2009; Fiedel 2000, 2004; Goebel et al. 2008; González-José and Bortolini 2011; Mazières 2011; O'Rourke 2011; O'Rourke and Raff 2010; Pitblado 2011).[6] Nonetheless, Powell's and Sutter's work represents a significant change in perspective and is relevant to the peopling of the New World discussion.

Powell's (1995, 1997, 2005) major contribution was focusing on older remains in his evaluation of New World prehistory. For example, he used

[6] Fiedel (2004:80) writes that "some later, marginal populations, such as the natives of Tierra del Fuego, have peculiar, archaic-looking traits (including Sundadont teeth)" but cites Lahr (1995), a more general review article, rather than Powell's work. Dillehay (2009) and Goebel et al. (2008) do cite Powell (2005), but they specifically cite his craniofacial, not dental, work. Fiedel (2000) cites Steele and Powell (1992, 1994, 2002) and Powell and Rose (1999).

a large sample of Middle Holocene Eastern Woodlands populations dating from ~8500 to 5000 BP in a series of multivariate statistical analyses. Using Turner's published trait frequencies as the training sample, discriminant function analysis allocated most Archaic period populations into the Sundadont category (Powell 1995). This was not a unique finding. Lahr and Haydenblit (1995) identified a Sundadont pattern based on four traits in a population from Tierra del Fuego (see also Lahr 1995), Haydenblit (1996) documented Sundadonty in a series of recent (1300 BC–AD 750) central Mexican samples using 29 dental traits, and Sutter (2005b, 2009b) observed that a number of Andean samples (Paleoindian, Preceramic, and Southern Cone Chilean) did not demonstrate a Sinodont pattern. Sutter's work (1997, 2000, 2005b, 2009b) is interesting because it ties Sinodonty in more recent Andean populations to biocultural evolutionary effects associated with emergent agriculture. He explains a north-to-south cline for the pattern and temporal trends for an increasingly Sinodont dentition as the result of demic diffusion from Mesoamerica, thus establishing the complex as a functional whole subject to selection mechanisms.

Powell (1997, 2005; Powell and Neves 1998) fine tuned his dissertation analyses and included a small sample of Paleoindian dentitions in his database. Multidimensional scaling of trait frequencies confirmed that early New World populations (Paleoindians from South America, North American Archaic populations) were not Sinodont. However, the use of less restrictive statistics (those that do not force an allocation into predetermined categories) also indicated that early Americans were not Sundadont, but rather formed their own distinct cluster. This patterning was demonstrated by Powell (1995: figures 8.5, 8.6, 8.7) for a series of North American Archaic samples (Powell, 1997: figure 3; 2005: figures 9.6, 9.7) with the inclusion of Paleoindians. Given the time spans included, such divergence should come as no surprise. Interestingly, the Archaic samples were not only divergent from modern Native American and Old World Sinodont and Sundadont samples but also from New World Paleoindians, particularly those from South America. UPGMA cluster analysis affirmed this distinction, with five clusters identified (North American Archaic, South American Paleoindian, Neolithic Siberia, modern Sinodonts, and modern Sundadonts) (Powell 2005:212). Powell's Paleoindian sample demonstrated higher frequencies of shoveling than Sinodonts and Sundadonts, double shoveling on par with Sinodonts, two traits that were intermediate between the two patterns (four-cusped LM2, three-rooted LM1), and several traits that were less frequent in Paleoindians than in either Sundadonts or Sinodonts (LM1 deflecting wrinkle, UM3 peg/absent, UM1 enamel extension, one-rooted UP1) (see Powell 2005:195). Sutter's (2009b:15) aggregate Andean Paleoindian sample affirms these differences, documenting no peg or agenetic

UM3s, no two-rooted UP1s, a low frequency of incisor winging, and no three-rooted LM1s. These results are contrary to Scott and Turner's (2006:65) claim that "all Native Americans, including all known Paleo-Indians, Archaic and later populations, and minimally admixed living individuals, possess only the Sinodont pattern."

How different scholars came to such distinct conclusions is puzzling. We considered the possibility that researchers included different Paleoindian dentitions in their respective samples.[7] This possibility might suggest that sample bias is affecting the perception of early New World morphological variability, particularly if a more complex, geographically structured series of migrations is responsible for the variation among different Paleoindian and Paleoamerican[8] skeletons. In other words, all assessments of Paleoindian dentition are correct in that stated trait frequencies are unbiased and accurate.

[7] Powell (1993) included each of the Paleoindian and Archaic specimens included in Turner's (1992a) analysis, but he used Turner's published raw data. Turner (1992a) and Powell (1997; Powell and Neves 1998) both included the Paleoindian skeletons from Gordon Creek, Colorado, and Lagoa Santa, Brazil, in their analyses of dental morphology. Additionally, Powell (2005) assessed the dental morphology of at least one Paleoindian specimen (Midland, Texas) and the cranial morphology of another (Pelican Rapids, Minnesota [Steele and Powell 1992, 1994]) included in Turner's (1992a) analysis, but it is not clear that Powell included these specimens in a published analysis of dental morphology. As Turner (1992a) published raw data from Paleoindian dentitions, it is clear which specimens Turner (1992a) assessed and included in his analyses. Turner (2002) later observed (but did not report raw data from) the Spirit Cave and Wizards Beach skeletons from Nevada. It is less clear which Paleoindian skeletons Powell assessed for dental morphology as he does not always identify which specimens compose his North American and South American Paleoindian samples (Powell 2005:211, fig. 9.7). While he tends to mention which Paleoindian specimens are included in craniofacial analyses (Powell 2005; Steele and Powell 1992, 1994, 2002), we cannot assume that the same specimens were included in analyses of dental morphology. Specimens examined by Powell for dental morphology and subjected to biodistance analysis include Paleoindian skeletons from Gordon Creek Colorado; Horn Shelter, Texas (although it is not clear whether both skeletons – No. 1 and No. 2. – were included in the analysis); Whitewater Draw (Sulphur Springs II), Arizona; and Wilson-Leonard, Texas (as reported in Powell 1997); skeletons from Lagoa Santa Cerca Grande 5 and 6, Lapa Vermelha IV, and Santana do Riacho I, all from Brazil (as reported in Powell and Neves 1998); and Kennewick Man (Powell and Rose 1999). Powell (2005) also observed the dentitions of Paleoindian skeletons from Grimes Point Burial Shelter, Nevada, and Shifting Sands, Texas, but it is not clear which, if any, analyses include discrete dental data from these individuals. The aforementioned specimens are likely an incomplete listing of Paleoindian skeletons assessed by Powell for dental morphological traits. Powell (2002:98) indicates that he has "examined over 500 individuals in North, South and Central America older than 8500yr B.P.," but he does not list the specimens examined or indicate whether cranial, dental, or both types of traits were assessed during examination. Similarly, Powell (1997:88) indicates that he, along with D. Gentry Steele, examined the teeth of more or less a dozen Paleoindian skeletons, but he does not provide a list of these specimens ("Junto com meu colega D. Gentry Steele, da Universidade A&M, do Texas, examinei os dentes de mais ou menos uma dúzia de esqueletos de paleoíndios (datados de 8.500 a 10.700 anos) encontrados na América do Norte (Figura 2)").

[8] See González-José et al. (2005) footnote 1 for discussion of the difference between the terms "Paleoindian" and "Paleoamerican."

Different interpretations of the *overall* record reflect incomplete sampling of a highly structured population of individuals that has been reified in modern usage by the term "Paleoindian." Such nuanced variation is something that an aggregate approach based on dichotomized trait frequencies interpreted with respect to the pan-Sinodont model alone would not identify.

Turner (2002, 2006; Turner and Scott 2007) refuted findings of New World Sundadonty on the basis of dental wear. His reasoning is that Sinodont dentition is characterized by *intensification* of crown and root features shared widely among Asian populations. Attrition removes these features, thus giving the false appearance of Sundadonty (see Burnett et al., this volume). However, there is no reason to question the data collection quality in the Powell, Haydenblit, and Sutter papers. Some specifically note discordant *root* trait frequencies as suggesting a Sundadont allocation (which should be unaffected by attrition – see Haydenblit 1996:237; Powell 1993:191), and Lahr and Haydenblit's (1995) analysis was based on four traits, two of which (UM3 peg molar, three-rooted LM1) are unaffected by wear. Powell (2005) (citing Powell et al. 1999) explicitly evaluated Turner's refutation by removing teeth with severe wear; earlier results suggesting Paleoindians were neither Sundadont nor Sinodont were supported.[9] In the end we are left wondering why wear does not just result in more missing data rather than Sundadont trait frequencies (and smaller sample sizes, easily recognized and often acknowledged). The issue of New World Sundadonty remains unresolved, despite the apparent ease with which mutual agreement could be achieved. This impasse suggests a final determination may not be particularly relevant to contemporary debates in the "peopling" literature.

17.4 Beyond Sinodonts and Sundadonts

Turner's dental morphological research laid the groundwork for a generation of scholars. The sheer quantity of data collection, efforts to advance testable models, and efforts to standardize data collection to facilitate global scale analyses are invaluable contributions to the field. However, the last 10 years has witnessed rapid advances in the peopling of the New World literature (cf. Fiedel 2000, 2004; Pitblado 2011). Pre-Clovis sites are now well established (e.g., Goebel et al. 2008; Waters et al. 2011). Researchers recognize a backflow of alleles (and people) into the Old World (de Azevedo et al. 2011; Ray

[9] It is unfortunate that the reference in Powell (2005) seems to be incorrect. The only Powell et al. (1999) cited in Powell (2005) is the article in *Antropologia Fisica Latinoamericana*; however, that article does not discuss dentition.

et al. 2010; Tamm et al. 2007; Zlojutro et al. 2006) and a significant "Beringian pause" that shaped the source population of New World peoples through genetic drift and partial geographic isolation (Fagundes et al. 2008; Hamilton and Buchanan 2010; Hubbe et al. 2011; Kitchen et al. 2008; Mulligan et al. 2008; Tamm et al. 2007). An early coastal route of migration is now accepted (Dixon 2001, 2011; Fagundes et al. 2008; Fix 2005; Goebel et al. 2008; Neves et al. 2003; Perego et al. 2009; Schurr and Sherry 2004; Turner 2002), and ancestral Clovis peoples are thought to have migrated south[10] from the same Beringian source population (Kemp and Schurr 2010) after the ice-free corridor opened about 1,000 years after deglaciation of the Pacific coast (Dixon 2011; Goebel et al. 2008; Perego et al. 2009; Pitblado 2011; Schurr and Sherry 2004). This same Beringian source may have divided (unintentionally) along the northern and southern (Aleutian) coasts of Beringia, thus resulting in two distinct waves of occupation down the Pacific and Atlantic coasts of North (and possibly South) America (O'Rourke 2011; O'Rourke and Raff 2010; see also Dillehay 2010; Neves et al. 2003; Yang et al. 2010).

Phenotypic variation continues to contribute to the New World origins debate, largely because craniometric research has become increasingly sophisticated, moving from initial typological approaches (e.g., Neves et al. 2004:494) to simulations and model testing (e.g., González-José et al. 2001:236–237). This recent work reflects a shift to a concern with process over typology and has consisted of explicit evaluation of a variety of influences on skull morphology ranging from the relative roles of evolutionary forces, to the plasticity of the skull due to climatic and diet variation, as well as differential response of regions of the skull to these influences (Barbeito-Andrés et al. 2011; de Azevedo et al. 2010, 2011; Dillehay 2003:24; Gonzalez et al. 2010; González-José and Bortolini 2001; González-José et al. 2008; Mazières 2011; Ousley and Jones 2010; Perez et al. 2007, 2009; Perez and Monteiro 2009; Pucciarelli et al. 2003, 2006, 2008, 2010; Relethford 2010; Strauss and Hubbe 2010). The continued importance of craniometry is in part due to the fact that the Howell's craniometric database is widely available online. Additional craniometric data continued to be published (e.g., Neves et al. 1999a), thus allowing researchers to implement more sophisticated craniometric analyses than was possible even 10 years ago.

However, despite recent new developments in the "peopling" literature, dental morphology's primary contributions remain the tripartite model, the

[10] Dixon (2011) suggests that people with Paleoindian technology (who had previously entered North America via a corridor along the Northwest coast) actually moved north from areas south of the continental glaciers taking the technology to eastern Beringia and contacting the inhabitants of eastern Beringia around 13,000 bp.

distinction between Sundadont and Sinodont populations, and typological assessment of population affinity within this dichotomized framework. The reality is that both dental complexes reflect minor variations on the same theme; differences are a matter of degree rather than absolute. The research approach remains somewhat coarse in comparison to what anthropological geneticists and craniometricians have recently put forth. And the omission of dental morphology from the most recent literature review (Pitblado 2011) reflects this stagnation.[11] The field as a whole, driven by developments in climate science, geology, archaeological discoveries, improved dating methods, advances in ancient DNA research, whole genome (mtDNA) modern DNA research, and recognition of fine-scaled resolution of genetic variation through haplogroup subclade typing, suggests the pan-Sinodont model simply lacks the specificity and nuance to contribute novel perspectives on those issues considered most pressing today. In short, describing all Paleoindians through modern Native Americans as Sinodonts does not allow us to evaluate the coastal and ice-free corridor two stage model (Perego et al. 2009; Pitblado 2011), evidence of a Beringian pause (Fagundes et al. 2008; Hamilton and Buchanan 2010; Kitchen et al. 2008; Mulligan et al. 2008; Tamm et al. 2007), or a bicoastal migration model (O'Rourke 2011; O'Rourke and Raff 2010) of Amerind expansion. The field has moved on.

However, none of the preceding should discourage future research on New World dental morphology. The dentition is every bit as useful as crania for inferring population history. As demonstrated throughout this volume, dentition preserves better, is subject to less developmental plasticity, develops early in life, is observable in subadult as well as adult remains, is not subject to postdepositional or cultural deformation (at least to the same degree as cranial form), is easy to score, and has the same degree of regional and global resolution as craniometric data (cf. Hanihara 2008; Hanihara and Ishida 2005; Irish and Guatelli-Steinberg 2003; Manica et al. 2007). Arguably, within the temporal scale of Native American history, dental traits behave like neutral loci. Model organism research on organogenesis is also very promising (Jernvall 2000; Jernvall and Jung 2000; Jernvall and Thesleff 2000; Kangas et al. 2004; Salazar-Ciudad and Jernvall 2002; Tucker et al. 2000, 2004); we have a realistic expectation of understanding the genetic structure and epigenetic pathways of dental variation that links observed phenotypes to specific genes and their

[11] Archaeologists and craniometricians seem entirely uninterested in dentition (Pitblado 2010; cf. Meltzer 2009). A review of the peopling literature from the last decade (Pitblado 2010) finds not a single reference to the tripartite model or dental data. Mazières (2011) presents a consensus model for the initial settlement of the Americas, and while he acknowledges the contribution of dental data to peopling models in the 1980s, his efforts to reconcile different peopling scenarios focus on those derived from molecular and craniometric data.

protein products. Initial efforts in this area are just now appearing (Hunter et al. 2010; Kimura et al. 2009). The two biggest concerns with dental morphological research are attrition and the less sophisticated ordinal and binary scale analytical approaches commonly used in the discipline. While we will never be able to reconstruct a canine distal accessory ridge removed by attrition, attempts to digitize morphological variation in metric form (e.g., Bunn et al. 2011) may lead to similar sophistication in data capture as seen in the fossil hominin literature (e.g., Benazzi et al. 2009; Skinner et al. 2009). Clearly, Dillehay's (2009:975) statement that "in recent years, researchers have turned from ancient tooth forms to comparative multivariate analyses of cranial morphology" must be corrected. To that end, the confrontational tone between morphologists studying dentition and crania (couched within a single vs. dual origins debate) is not productive. Evolutionary explanations of divergent evolutionary signals should be embraced rather than explained away in terms of differential data quality. With these details in mind, we present a preliminary analysis of Paleoindian dentition to demonstrate potentially useful research directions that move beyond the Sinodont/Sundadont dichotomy.

17.5 Analysis of interindividual Paleoindian variability

Despite the depth of the dental literature, there is one type of analysis that we have never seen published – that focusing on individual level variation among known and confirmed Paleoindian skeletons. Such particularistic, fossil-based studies have been published for crania (see Chatters 2000; Hubbe et al. 2007; Mizoguchi 2011; Neves et al. 1999a, b, c, 2003, 2004, 2005, 2007b; Neves and Blum 2000; Owsley et al. 2010; Powell 2005; Steele and Powell 2002), and the lack of dental equivalents is curious. Correcting this oversight may provide new perspectives on dental variation among the earliest Americans in ways that aggregate sample analysis (the norm) cannot. An interindividual, fossil-based approach can be used to evaluate competing models of geographically structured New World migration routes (coastal vs. ice-free corridor, bicoastal migration routes) and different migration processes (South America bottlenecking). In addition, considering variation among individuals with respect to geography allows one to evaluate whether it was ever prudent to combine such disparate samples into a large hemispheric aggregate ("Paleoindian") in the first place.

The first step in this meta-analysis was to confirm the Paleoindian status of published skeletons.[12] For example, we were unable to verify the age of (and

[12] Different definitions of Paleoindian skeletons versus Archaic skeletons abound in the literature (reviewed by Young 1988). Most scholars use these terms to refer strictly to the antiquity of

in some cases the existence of)[13] several of Turner's (1992a) Paleoindian listings while others are no longer considered Paleoindian in age. Nonetheless, Turner's data set provides the baseline to which other raw published data from confirmed Paleoindians were added (Chatters 2000; Jenks 1937; Owsley et al. 2010; Potter et al. 2011; Powell and Rose 1999; Young 1988). These individuals are summarized in Table 17.1.

Raw data on published morphological features were analyzed using Clustan, a multivariate cluster analysis program that calculates similarities or distances among objects without prior data imputation. Gower similarity coefficients were used because they are amenable to mixed data types (in this case, ordinal and binary scale) and can be estimated among all pairwise combinations of individuals. Similarities were visualized using multidimensional scaling (MDS) sets for two dimensions with 500 trials and 500 maximum iterations. Although missing data did not impede the analytical calculations, individuals with sparse cells were culled to prevent the pattern of missing data from affecting the results. In addition, the number of variables actually used in the analysis was drastically reduced. Variables with no interindividual variation and those that were autapomorphic (different in only one individual) added no content to the analysis and were eliminated. In addition, because distances are not conditioned by a covariance matrix, intertrait correlation can be problematic. Therefore, trait elimination was performed informally considering odontogenesis and trait homology. Trait selection was based solely on logistical concerns without consideration of "key" features that dominate past literature. Variable and individual selection was balanced to maximize Paleoindian representation and the strength of the phenetic signal.

We first considered patterns of variation among all North and South American Paleoindians. This analysis was limited by the lack of paired maxillae and

skeletons rather than referring to presumed or documented cultural practices, particularly subsistence economy (Steele and Powell 1994). It is widely agreed that skeletons dating to the Late Pleistocene (older than 10,000 yr BP) are considered Paleoindian. However, different chronological cutoffs are used for Early Holocene skeletons. Steele and Powell (Powell 2005; Steele and Powell 1992, 1993, 1994, 2002) use 8,500 yr BP as their breakpoint; skeletons older than this are typically considered Paleoindian, while those more recent than 8,000 BP are considered Archaic. Others use 8,000 BP as a cutoff (Sutter 2009b; Young 1988; Young et al. 1987). Recognizing that differentiating Paleoindian versus Archaic skeletons is somewhat arbitrary, we follow Fiedel (2000, 2004; see also Jantz and Owsley 2001; Turner 1992a) and use a more inclusive approach. We include Early Holocene skeletons that date to between 10,000 and 7,000 yr BP as Paleoindian but distinguish these from Late Pleistocene skeletons.

[13] This does not imply the data are manufactured, only that we could find no subsequent mention of these individuals in any publication that purports to summarize the existing Paleoindian database. These include the skeletons identified as Columbus, Nebraska; Savannah, Georgia; and Schutz Cave, Texas.

Table 17.1. *Early skeletal remains from North and South America*

Sample/site	Age (^{14}C years BP)	N	References
North America			
Upward Sun River, AK	~11,500	1	Potter et al. (2011)
Witt Site (Tulare Lake), CA	11,380 +/–70		Willig (1991)
Arlington Springs, CA	10,960 +/– 110 10,080 +/– 810 10,000 +/– 310	1	Berger and Protsch (1989); Johnson et al. (2002); Orr (1962)
Peñón Woman III, Mexico	10,755 +/–75	1	González et al. (2003, 2006); Jiménez López et al. (2006)
Anzick, MT	10,680 +/– 50 (average)	2	Owsley and Hunt (2001); Stafford et al. (1991)
Buhl, ID	10,675 +/– 95	1	Green et al. (1998)
Wilson-Leonard, TX	10,500–10,000	1	Steele (1998)
Chimalhuacán, Mexico	ca. 10,500	1	González-José et al. (2008); Lascuráin Ledesma et al. (2006)
Mostin, CA	10,470 +/–490	1	Taylor et al. (1985)
Warm Mineral Springs, FL[a]	10,260 +/– 190	1	Clausen et al. (1975); Turner (1992a)
Arch Lake, NM[a]	10,220 +/– 50; 8,870 +/– 40	1	Owsley et al. (2010)
Tlapacoya I, Mexico	10,200 +/–65	1	González et al. (2003, 2006)
Marmes, WA	10,130 +/– 300; 9,840 +/–300 9,820 +/–300	3	Oakley et al. (1975); Sheppard et al. (1987)
Midland, TX[a]	ca. 10,000	1	Holliday and Meltzer (1996); Stewart (1955); Turner (1992a); Young (1988)
White Water Draw, AZ	10,000–8,000	1	Waters (1986)
J.C. Putnam, TX	-[b]	1	Stewart (1945)
Horn Shelter, TX[a]	9,875 +/– 110 (average)	2	Owsley et al. (2010); Young (1988)
49-PET-408 (On Your Knees Cave), AK	9,730 +/– 40 (average)	1	Dixon (1999); Taylor (2006)
Grimes Point Burial Shelter, NV	9,470 +/–60		Tuohy and Dansie (1997)
Gordon Creek, CO[a]	9,455 +/– 110 (average)	1	Breternitz et al. (1971); Turner (1992a)
Spirit Cave, NV	9,415 +/– 25 (average)	1	Edgar (1997); Jantz and Owsley (1997)
Wizard's Beach, NV	9,225 +/– 60 (average)	1	Edgar (1997); Dansie and Jerrems (2006)
Browns Valley, MN	9,049–8,790 +/– 11,0/82	1	Jenks (1937); Myster and O'Connell (1997)
LaBrea, CA	9,000 +/– 80	1	Berger (1975); Kroeber (1962)
Renier, WI	ca. 9,000–8,000		Mason and Irwin (1960)

(*continued*)

Table 17.1. (*cont.*)

Sample/site	Age (^{14}C years BP)	N	References
Metro Balderas, Mexico	ca. 9,000	1	González-José et al. (2008); Lascuráin Ledesma et al. (2006)
Cueva de Tecolote, Mexico	ca. 9,000–7,000	1	González-José et al. (2005)
Koster (Horizon 11), IL	ca. 8,500		Struever and Holton (1979)
Tehuacan (El Riego), Mexico[a]	ca. 8,500–7,000	1	Anderson (1967); Turner (1992a)
Kennewick, WA	8,410 +/– 60 (average)	1	Powell and Rose (1999)
Fishbone Cave, NV	8,370 +/– 50; 8,220 +/– 50	1	Dansie and Jerrems (2006)
Gore Creek, BC	8,250 +/– 115	1	Cybulski et al. (1981)
Hourglass Cave, CO	8,170 +/–100; 7944 +/–84 7,714 +/–77		Mosch and Watson (1997)
Windover, FL	8,120–6,990		Doran and Dickel (1988); Doran (2002)
Pelican Rapids, MN[a]	7,840 +/– 70	1	Myster and O'Connell (1997); Jenks (1937); Turner (1992a)
L'Anse Amour, Labrador	7,530 +/–140		Tuck and McGhee (1976)
Texcal Cave, Mexico	7,480 +/–55	1	González et al. (2003, 2006)
Anderson, TN	7,180–6,495		Dowd (1989); Powell (1995)
Eva, TN	7,150 +/–500		Lewis and Kneberg Lewis (1961); Powell (1995)
Shifting Sands, TX	–	1	Powell (2005)
South America			
Lapa Vermelha IV (Luzia), Brazil	11,680 +/–500 – 10,200 +/–220 9,330 +/–60 (minimum age)	1	Gruhn (1991); Powell and Neves (1998); Prous and Fogaça (1999)
Cerca Grande 6 and 7, Lagoa Santa, Brazil[a]	ca. 11,000–8,000	44	Neves et al. (2004, 2005); Turner (1992a)
Pampa de Fosiles 13, Peru	10,250 +/–180	2	Chauchat (1988)
Sueva 1, Colombia	10,090 +/–90	1	Correal Urrego and van der Hammen (1979)
Quiqche Cave Tomb 1, Peru	9,940 +/–200[c]		Beynon and Siegel (1981)
Toca dos Coqueiros, Brazil	9,870 +/–50	1	Lessa and Guidon (2002)
Tequendama, Colombia	9,740 +/–135	9	Correal Urrego and van der Hammen (1977)
Toca da Janela da Barra do Antoniao, Brazil	9,670 +/–140		Lessa and Guidon (2002)
Santana do Riacho Burial XII, Brazil	9,460 +/–110	1	Neves et al. (2003); Powell and Neves (1999); Prous (1992); Prous and Fogaça (1999)
Guavio 1, Colombia	9,360 +/–45	1	Correal Urrego and van der Hammen (1979)

Table 17.1. (*cont.*)

Sample/site	Age (^{14}C years BP)	N	References
Piuquenes Cave, Chile	8,990 +/–40		Mena L. et al. (2003)
Acha, Chile	8,970 +/–255		Arriaza (1995); Mena L. et al. (2003)
Baño Nuevo-1 Cave, Chile	8,890 +/–90; 8,880 +/–50 8,850 +/–50	5	Mena L. et al. (2003)
Capelinha Burial II (Luzio), Brazil	8,860 +/–60	1	Neves et al. (2005)
Santo Domingo Tomb 1, Peru	8,830 +/–190		Beynon and Siegel (1981)
Pali Aike, Chile	ca. 8800?	4	González et al. (2003); Mena L. et al. (2003); Turner (1992a); Turner and Bird (1981)
Arroyo Seco, Argentina	8,560 +/–320; 7,800 +/–115; 7,615 +/–90; 5,250 +/–110		Politis and Madrid (2001)
Santana do Riacho, Brazil	8,280 +/–40; 8,185 +/–110	40	Neves et al. (2003); Powell and Neves (1999); Prous (1992); Prous and Fogaça (1999)
Las Vegas, Ecuador	8,250–6,600	192	Stothert (1985)
Sumidouro Cave, Lagoa Santa, Brazil	>8,000	29	Neves et al. (2007a)
Huentelauquen-2, Chile	8,080 +/–70		Mena L. et al. (2003)
Cuchipuy, Chile[a]	8,070–6,105; c. 8,000–6,000	3	Santoro et al. (2005); Turner (1992a)
Intihausi, Argentina	8,060 +/–100; 7,970 +/–100	6	Oakley et al. (1975)
Tres Ventanas Tomb 1, Peru	8,030 +/–130		Beynon and Siegel (1981)
Checua, Colombia	7,800 +/–60 – 6,800 +/–40	4	González-José et al. (2008)
Santo Domingo Tomb 2, Peru	7,740 +/–85	1	Beynon and Siegel (1981)
Camarones, Chile	ca. 7,000	1	Arriaza (1995)

Notes:
[a] Skeleton included in analysis in the present study.
[b] Associated with stratum thought to date to the Late Pleistocene (Young 1988).
[c] Date is from the level underlying the skeletal remains.

mandibulae for Lagoa Santa, an indispensible sample. Therefore, only maxillary data were used, totaling six traits observed for a sample of 15 individuals (UI1 shoveling, hypocone UM1, Carabelli UM1, enamel extension UM1, root number UP1, root number UM2). The sample included six North American dentitions (Warm Mineral Springs for the east coast, Pelican Rapids, Gordon

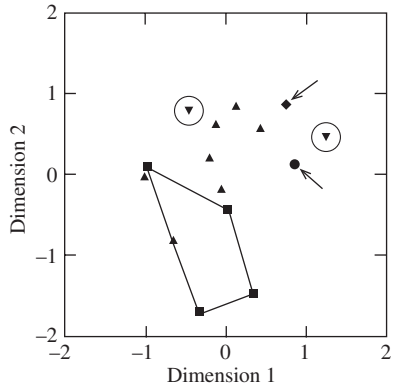

Figure 17.2. Multidimensional scaling output from Clustan based on Gower similarity coefficients calculated from six maxillary dental morphological traits for confirmed North and South American Paleoindians. Icons represent geographic divisions: circle = Mexico, diamond = eastern North America, square = central North America, upward triangle = eastern South America, downward triangle = western South America.

Creek, Arch Lake and Horn Shelter 2 from the middle of the continental United States, and Tehuacan Tc50–2 from Mexico), two individuals from the west coast of South America (Cuchipuy 9, 10), and seven individuals from Lagoa Santa (2352, P-2, P-5, comp 2, 3, 4, 5) in eastern South America.

Multidimensional scaling of Gower similarity coefficients is presented in Figure 17.2. Although by no means discrete, the major geographic divisions of Paleoindians for which we have more than one data point do exhibit a clustering tendency. West coast South American Paleoindians from Cuchipuy fall within the positive half of dimension 2 but are diffuse along dimension 1, east coast South Americans from Lagoa Santa tend to fall near the middle of both axes, while North American Paleoindians fall near the center of the dimension 1 axis but within the negative axis of dimension 2. The one exception is the single individual from eastern North America (Warm Mineral Springs) which is similar to South American individuals but quite distinct from other North American Paleoindians. Unfortunately, MDS in Clustan does not produce output that would allow assessment of what variation along these dimensions represents. Nonetheless, there is geographic patterning evident. When compared by continent, differences between North and South American Paleoindians are significant for dimension 2 at the 10 percent level ($p = .081$); dimension 1 was not significant ($p = .919$). East versus west coast South Americans exhibited no significant differences; however, the latter sample contains only two individuals and statistical power was minimal. We note the single individual from

Mexico is most similar to the South American Paleoindians. Lagoa Santa displays about as much interindividual variability along both dimensions as the central United States sample. This could reflect an extremely diverse population of Paleoindians in eastern South America during the early Holocene or an extremely homogeneous population of Paleoindians from North America during the same interval. We note that the one clear outlier among the North American individuals is from Warm Mineral Springs, Florida. Affinity between this individual and South American Paleoindians may reflect a bicoastal migration route *sensu* O'Rourke and Raff (2010) or a combined bicoastal migration (north and south coasts of Beringia eventually into the Pacific and Atlantic coasts of North America) with a later migration through the ice-free corridor (the central North Americans in this analysis). Additional data are needed to evaluate this possibility.

To consider patterns of variation among North American Paleoindians further we repeated the analysis using only North American individuals. Eight variables were used (shoveling, UM1 hypocone, UM1 Carabelli, UM1 enamel extension, root number UP1, root number UM2, cusp number LM2, root number LM2) for a sample of six individuals (Pelican Rapids, Gordon Creek, Warm Mineral Springs, Arch Lake, Horn Shelter 2, Kennewick). The inclusion of Kennewick allows us to compare variation between the Pacific (Kennewick) and Atlantic (Warm Mineral Springs) coasts as well as the U.S. midlands. All data were imported into Clustan and analyzed as earlier, with results presented in Figure 17.3. Geographic patterning is evident, with central North Americans dominating the upper right quadrant of the plot and both coastal individuals located in the bottom left quadrant of the plot. The distinction between the central North American Paleoindians and Warm Mineral Springs documented in Figure 17.3 is confirmed with this broader analysis inclusive of more dental traits. The similarity between Kennewick and Warm Mineral Springs is contrary to a bicoastal model in which small populations radiated from Beringia along the eastern and western coasts of North America. In fact, Kennewick and Warm Mineral Springs are the most geographically dispersed fossils in the analysis, yet they maintain relatively similar dental profiles. The dental morphological distinction between coastal and interior North American Paleoindians evident in Figure 17.3 is also evident, to an extent, in Figure 17.2. In other words, coastal Paleoindians from both North and South America appear to be relatively homogeneous and distinct from North American Paleoindians from Colorado, Minnesota, New Mexico, and Texas. These results are intriguing in light of recent suggestions of an earlier coastal, and later ice-free corridor route of entry into North America. Perhaps the geographical differences represented in Figure 17.3 are reflective of this population history.

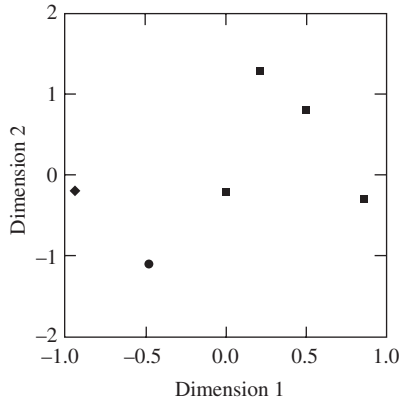

Figure 17.3. Multidimensional scaling output from Clustan based on Gower similarity coefficients calculated from eight dental morphological traits for confirmed North American Paleoindians. Icons represent geographic divisions: circle = western North America (Kennewick), square = central North America, diamond = eastern North America (Warm Mineral Springs).

It is impossible to know the effects of time on these results as we have compressed several thousand years into a momentary population.[14] However, even this simple analysis using a handful of traits culled from the published literature analyzed with the least sophisticated statistics available demonstrates geographical patterning that coincides with existing hypotheses about the peopling of the New World. We hope this represents, at the very least, a new starting point for future research and discussion.

17.6 Dental morphology as bioarchaeology

As is evident from the preceding review, much seminal research on New World dental morphology has been concerned with large-scale questions of Native American origins. In the same way that current research about peopling of the Americas has begun to move past questions of Sinodonty and Sundadonty, the study of dental morphology in the Americas is increasingly employed to address questions on smaller scales. Here, the emphasis is more contextual and less driven by explicit inferences of migration and evolutionary mechanisms. It is more culturally oriented bioarchaeology than skeletal biology. It is more population-based than racial. Following Buikstra et al.'s (1990) scale-based

[14] Among the Paleoindian skeletons included here the oldest date is 10,220 +/- 50 BP and the most recent dates to 7,580–7,140 BP.

division of contemporary biodistance research, in this section we summarize key literature that uses dental morphology to infer population structure at the regional level as well as various intracemetery or intrasite approaches that infer cemetery structure, postmarital residence, or relative relatedness among skeletons (kinship). Both are expansive literatures and this is not the place for a comprehensive review. Rather we select key studies that embrace the contextual elements of bioarchaeological biodistance analysis in a way that complements the migration and evolutionary focus of the first half of this chapter.

17.6.1 Regional approaches

Regional scale analyses of dental morphology assess patterns of affinity among a series of near-contemporary samples. Purely descriptive (read historical) research, however, may suffer from providing answers in search of a question; removed from a larger narrative framework (like peopling of the Americas) such particularistic studies have limited anthropological impact. Exceptions include studies in the southwestern United States that contribute to resolving issues of cultural patrimony while also writing the primary history of recent population movements (Scott and Dahlberg 1982; Scott et al. 1983, 1988). Such endeavors are of direct relevance to descendant communities and are almost uniquely southwestern in focus because of the clear linkage among prehistoric, historic, and modern southwestern peoples. Griffin's (Griffin 1993; Griffin et al. 2001) work on colonial period populations from the southeastern United States also ties into a larger anthropological framework – that of colonialism. Regional patterns of morphological variation were interpreted among a series of precontact and postcontact samples from eastern North America with respect to changing sociopolitical dynamics after establishment of Spanish missions and later English colonies along the Atlantic coast. Levels of morphological diversity were also used to infer changing demographic characteristics of postcontact populations. For example, late mission period samples reflected reduced variability due to the effects of epidemic disease, declining population size, and the loss of alleles due to genetic drift. These are just two examples where morphological biodistance research contributes to a larger research question within a bioarchaeological interpretive framework.

Sutter's work in the Andes is most exemplary of the potential for dental morphology to contribute to large- and small-scale issues when contextualized within a specific regional focus.[15] In addition to his contributions to the

[15] While the bulk of Sutter's research in the south central Andes uses dental morphological traits as proxies for genetic relatedness (1997, 1999, 2000, 2005b, 2006, 2009a, b; Sutter and Sharratt

peopling of the Andes, a central theme in Sutter's bioarchaeological work is the biocultural consequences of pre-Inka state expansion and collapse, particularly with respect to the Middle Horizon Tiwanaku polity in the Lake Titicaca Basin. His research on Moquequa and Azapa Valley populations uses dental morphological data to investigate the nature of Tiwanaku influence in the peripheral Azapa Valley as well as to infer the nature of population stability with the emergence of Chiribaya and Tumilaca polities in the Moquequa Valley. Although we emphasize the biological aspects of this work here, it is important to note that he interpreted his results by blending social identity and microevolutionary theory contextualized within the regional archaeological literature. For example, he identified long-term population continuity in the Azapa Valley (Sutter 1997, 2000, 2005a, 2006, 2009b) with gradual *in situ* microevolution of local populations, but with decreasing genetic isolation through time. During later periods, Azapa Valley populations became more similar to the altiplano Tiwanaku sample, suggesting limited genetic input. These results imply that Tiwanaku influence in the Azapa Valley was primarily cultural in nature, consistent with a model of indirect exchange of goods and ideas without substantial gene flow or colonization (Sutter 1997, 2000, 2005a, 2006, 2009b); thus, novel data were provided on the way that states, as imperialistic entities, exert control over peripheral political formations.

Sutter's research has also been concerned with ethnicity, beginning with establishing bioarchaeological criteria for identifying nonlocal ethnic groups in the archaeological record and expanding to consider more nuanced subjects such as ethnogenesis, the emergence or formation of new social identities (Sutter 1997, 2000, 2005a; 2009a, b; Sutter and Sharratt, 2010). For example, the origins of the Late Intermediate Period Chiribaya and Tumilaca polities have been debated, with some suggesting the Chiribaya, a coastal polity in the lower Moquegua Valley, represents an indigenous coastal formation (Buikstra et al. 2005; Lozada 1998; Lozada and Buikstra 2005). In contrast, dental morphological analyses, combined with archaeological data, suggest the Chiribaya (Sutter 1997, 2000, 2009a, b) and Tumilaca (Sutter 2009a; Sutter and Sharratt 2010) emerged after the dispersal of inhabitants from the Moquegua Valley to the coast with the decline of Tiwanaku's influence. Thus, archaeological and biological data suggest Chiribaya and Tumilaca traditions reflect newly emerging social identities (ethnogenesis) during a time of political and economic transition (terminal Middle Horizon) that coalesced into somewhat stable sociopolitical entities that persisted for several centuries after the collapse of the Tiwanaku state. Sutter's work is notable for its temporal depth, comparative

2010), his biodistance research is not limited to dental morphology alone (see Sutter 2005a; Sutter and Mertz 2004).

nature, and use of multiple lines of evidence to test models derived from archaeological data.

17.6.2 Intracemetery approaches

Intracemetery research is another area where dental morphology has made significant contributions to the study of New World populations. This immense literature has been the subject of recent review (see Stojanowski and Schillaci 2006); only a summary is presented here. Such particularistic studies provide a variety of inferences about past populations including (1) using sample variability to infer the composition of the population that used a cemetery; (2) considering temporal microchronological variation in morphology and relating such changes to population structure, demographic structure, or in-migration; (3) using age cohort analysis to infer natural selection for specific phenotypes; (4) examining overall cemetery structure and linking variation in morphological signatures to social organization; (5) inferring postmarital residence practices that index a number of other social variables often not visible in the archaeological record; and (6) identifying close kin in archaeological sites (often in a human interest capacity). Multiple lines of evidence, including craniometric and cranial nonmetric traits, odontometrics, postcranial nonmetric traits, digital pattern profiles, frontal sinus patterns, and biomolecular approaches such as paleoserology and, most visibly, ancient DNA, have been used for intracemetery analyses in various contexts throughout the world (see Stojanowski and Schillaci 2006:56 for review). Here we focus only on those that use dental morphology in New World populations.

The majority of these studies emphasized identifying evidence of kinship in archaeological assemblages or establishing the degree of relatedness among segments of mortuary samples (Christensen 1998; Corruccini and Shimada 2002; Duncan 2009, 2012; Hammond et al. 1975; Howell and Kintigh 1996; Jacobi 1996, 1997, 2000; McClelland 2003; Pietrusewsky and Douglas 1992; Spence 1996). Often such inferences are linked to higher order anthropological questions. For example, Corruccini and Shimada (2002) used the pattern of dental morphology among graves at the site of Huaca Loro in Peru to confirm that the site represented an elite cemetery whose organization was well planned. This speaks to regional issues of state formation and ascribed status. Howell and Kintigh (1996) targeted elements of social organization above the level of the individual family in their analysis of dental variation at Hawikku. They confirmed that different lineage groups used different parts of the cemetery for burial of the dead, which they then linked to political structure and an ascribed status with respect to leadership positions within the community. This

research, therefore, addresses the origins and development of social inequality. Duncan's work (2011) also used morphological data and intracemetery methods to inform a broader anthropological issue. In this case, dental morphology was used to identify relatedness among skulls from mortuary deposits in the contested Petén Lakes region of northern Guatemala. The archaeological context suggests the remains were interred as part of a sacrificial performance that would have been a public spectacle designed to accentuate the humiliation of war victims while harkening back to past glories at the site. The work, then, helps define the political climate of the Postclassic period Maya by showing that certain social lines were drawn, in part, on the basis of kinship.

Finally, both Stojanowski and Schillaci (2006) and Tomczak and Powell (2003) used intracemetery methods to investigate social organization and cemetery structure at the Early Archaic period Windover pond site located in Brevard County, Florida. Although the studies drew somewhat different conclusions, they shared the same goal of using sex-specific variation and spatial patterning of morphological data to understand how the cemetery was used and structured by Native Americans almost 8,000 years ago, and what this structure suggests about the group or groups that used the pond as a cemetery. Results from biodistance analyses were filtered through the lens of comparative hunter-gatherer ethnographic studies and Archaic period archaeology of the southeastern United States. Sex-specific differences in the degree of morphological variation suggest a patrilocal residence pattern and spatial analysis of morphological traits indicated control of segments of the pond by different lineage groups for burial of the dead. Interestingly, rare dental traits clustered spatially, but not in the sense of proximity but rather in terms of the directionality of the patterning. In particular, rare traits were found in individuals in rows aligned perpendicular to the pond margin, which suggested seasonal variation in pond water levels precluded placing closely related individuals in close physical proximity in some cases. Perhaps most intriguing was the association between different weaving styles (bodies were wrapped in mats before being buried) and certain rare morphological features. This suggests the presence of kin-structured weaving groups or traditions at this early age of Native American history.

We mention Windover in closing because the site reflects the dual nature of how morphological data can be used to study the Native American past. Powell (1995, 2005; Tomczak and Powell 2003), for example, considered postmarital residence practices at Windover but also used the sample for broader research questions, specifically addressing whether the population presented Sinodont or Sundadont morphology. And this duality highlights an important, concluding point. Although seemingly site-focused, intracemetery analyses are related

to broader narratives such as New World origins because they inform baseline issues on sample composition that could have a significant impact on our view of the deep past. In particular, Early American studies must be cognizant of the grave potential for mortuary sampling bias to skew our interpretation of group biology, and only a focused bioarchaeological and archaeological analysis can infer such levels of detail. Therefore, the analyses of Windover demonstrate a combined bottom-up and top-down approach focusing on a unique site that provides unparalleled insights into the peoples that first occupied this hemisphere.

17.7 Conclusions

This chapter has provided a brief overview of the history of dental morphological research on the native peoples of the Americas. We have emphasized intracemetery, regional, and continental scales of analysis, focusing most heavily on the extensive literature on First Americans research. In addition, we have presented a brief and simple analysis of Paleoindian interindividual variation. This analysis documented regional clustering of individual Paleoindian skeletons consistent with the predictions of specific migration scenarios generated from mitochondrial DNA variation among contemporary populations. In particular, coastal North American Paleoindians were fairly distinct from other North American Paleoindians, and, with the exception of the Warm Mineral Springs skeleton, the North American Paleoindians were fairly distinct from all South American Paleoindians. Such geographical patterning may be consistent with microevolutionary changes in a Beringian source population from which two pulses expanded: the first a coastal route down into South America and the second an interior route through the ice-free corridor. Of course, this inference is based on few individuals and a handful of traits. The list of confirmed Paleoindian skeletons is expanding (see Table 17.1) and a systematic dental survey of known individuals is now long overdue. Other related areas for methodological research will help dental morphology on all three scales of analysis that we discuss here. Data collection must move beyond the ASUDAS, however. The limited number of skeletons warrants high-resolution digital data capture techniques such as those used in paleoanthropology. Data analysis must also move beyond dichotomized trait frequencies that eliminate potentially useful variation. While the list of Paleoindian skeletons is growing, it is by no means expansive and a fossil-based approach that maximizes data sensitivity and density, regardless of preservation and wear, is necessary if dental morphology is to reinsert itself into the First Americans literature.

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18 *Crown morphology of Malay deciduous teeth: trait frequencies and biological affinities*

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18.1 Introduction

Variation in morphological attributes of deciduous teeth has been documented for a disparate global assortment of human populations past and present. Despite the potential significance for answering key questions of biological affinity and patterning of dental variation through space and time, deciduous nonmetric traits of modern populations in insular Southeast Asia have not been documented. This investigation in a sample of Javanese Malay is designed to achieve the following objectives: (1) document the range of expression and frequency of nonmetric tooth crown traits; (2) compare nonmetric trait frequencies of the Javanese dental sample with a global sample of modern and prehistoric groups; (3) assess biological affinities of the Javanese sample with proximal East and South Asian groups, as well as with a diverse global sample; and (4) determine whether the Javanese Malay deciduous dental pattern is consistent with the Sundadont dental complex by identifying shared and distinctive features.

Population studies of deciduous tooth crown and root morphology have been conducted for recent European (Jørgensen 1955), sub-Saharan African (Grine 1986, 1990), South Asian (Kaul and Prakash 1981, 1984), and East Asian (Hanihara 1966, 1968) samples. Nonmetric morphological variation of deciduous teeth in archaeologically derived samples has been reported for Native North Americans of the Ohio River Valley (Sciulli 1977, 1990; 1998), Near Eastern groups (Smith 1976, 1978); East Asians, including Ainu, Jomon, and Japanese (Kitagawa et al. 1995; Kitagawa 2000); and South Asians from the Chalcolithic site of Inamgaon, located in the Deccan Plateau of western India (Lukacs and Walimbe 1984). Finally, nonmetric variation in African and Asian

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samples of early hominin deciduous teeth has been extensively described and compared (Grine 1984, 1985).

Insular Southeast Asia is an important geographic region for anthropological inquiry. Postglacial climate and changing sea levels contribute to the discontinuous distribution of human populations across this island archipelago and have enhanced intergroup isolation accentuating biological and cultural diversity (Soares et al. 2008). In addition, the early dispersal of modern humans from Africa along the southern, coastal migration route along the Indian subcontinent is hypothesized to have passed directly through Southeast Asia and into Australia (Macaulay et al. 2005; Mellars 2006). Recent and early historic archaeology attests to the movement of peoples and cultures from South Asia east and south into the Indonesian archipelago. Given the anthropological significance of the region, it is surprising that dental nonmetric morphological variation has not been extensively documented for populations of Southeast Asia generally, or for Indonesia in particular.

18.2 Materials and methods

This research was conducted by observing crown morphology in stone plaster dental casts of Javanese Malay schoolchildren from the city of Yogyakarta (Java, Indonesia; Figure 18.1). Indonesia comprises two main and many subsidiary ethnic groups of anthropological and clinical interest. They are the Austro-Melanesian and the Malay. Ethnically the sample under investigation consists of Malay, a name referring to the main inhabitants of Indonesia north and west of Wallace's line. The Malay in this study are all from south-central Java, in the city of Yogyakarta. The sample of 142 individuals is composed of 61 females (42 percent) and 81 males (57 percent). It was randomly selected from a larger collection of dental impressions (n = 297) made from children attending 38 kindergartens in Yogyakarta. The casts were made by Sri Kuswandari in 2001–2002, for a collaborative study of primary tooth crown odontometry (Kuswandari and Nishino 2004) and interdental spacing (Kuswandari et al. 2006). Informed consent of children's parents was obtained prior to collecting data, making dental impressions, and pouring stone plaster dental casts. This study subsample and the larger original collection of casts are similar in representation by sex (female = 137, 46.1 percent; male = 160, 53.9 percent) and mean age at examination (Table 18.1).

Stone plaster casts of the full maxillary and mandibular dental arcades were examined under background fluorescent and focused incandescent light. Observations included macroscopic visual assessment supplemented by

Table 18.1. *Mean age (in years) of subjects at examination in original sample and this study sample*

		This study (subsample)		
Variable	Original sample[a]	Sex-pooled	Female	Male
n	297	142	61	81
mean	5.21 yr	5.2 yr	5.0 yr	5.3 yr
sd	0.65	0.7	0.7	0.6
min	3.3	3.3	3.3	4.0
max	6.6	6.5	6.4	6.5

Note:
[a] Kuswandari and Nishino (2004).

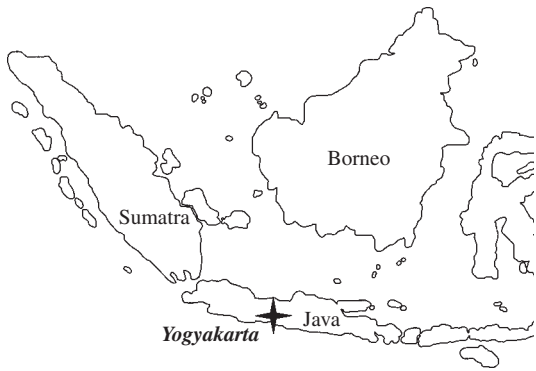


Figure 18.1. Location map.

examination with hand lenses of 5 and 10 power magnification. Morphological observations followed procedures described by Hanihara (1961) and modified by Sciulli (1998) and others (see Appendix for details of trait classification). Digital photographs were made of the occlusal surfaces of all specimens using a Fuji FinePix – S2 Pro (SLR with interchangeable lenses), a Tamron 28–200 mm macro lens, and Kenko Uniplus extension tubes (N-AF, 12 and 25 mm). In the analysis of crown morphology in the permanent teeth, male and female data are often pooled in calculating trait frequencies. Absence of sex dimorphism is often assumed without statistically testing each trait for significant sex differences. Because nonmetric dental attributes may exhibit variable patterns of sex dimorphism by trait in different samples, we tested for sex differences in trait frequencies prior to pooling male and female data.

Table 18.2. *Trait frequencies by sex with tests of significance*

			Male		Female		
Trait	Tooth	Cutoff	f	n	f	n	p
Maxillary dental traits							
Shovel shape	udi1	≥ 1	0.545	77	0.519	52	0.8912
	udi2	≥ 1	0.836	73	0.931	58	0.0306*
	udc	≥ 1	0.691	81	0.746	59	0.6023
Talon cusp	udc	≥ 1	0.234	85	0.016	63	1.000 (Fet)**
Tuber dentale	udc	≥ 1	0.263	80	0.317	60	0.2869
Conical crown	udc	+	0.075	80	0.017	59	0.2384 (Fet)
Parastyle	udm1	3	0.024	85	0.048	63	0.7237
Cusp number	udm1	4-, 4	0.210	81	0.203	59	0.3505
Hypocone	udm2	4	0.803	81	0.864	59	0.3370
Carabelli's	udm2	≥ 3	0.238	84	0.143	63	0.0216*
Cusp 5	udm2	≥ 1	0.084	83	0.065	62	0.7670
Mandibular dental traits							
Winging	ldi1	= 1	0.266	64	0.415	41	0.3041
Shovel shape	ldi1–2, ldc	≥ 1	0.385	78	0.316	57	0.7064
Conical crown	ldc	+	0.013	80	0.017	58	0.8111 (Fet)
Triangle crown	ldm1	+	0.062	81	0.069	58	0.8642
Cusp number	ldm1	= 5	0.593	81	0.690	58	0.1218
Groove form	ldm2	Y	0.943	52	0.955	45	0.9068
Cusp 5	ldm2	= 5	0.284	81	0.293	58	0.9303
Cusp 6	ldm2	≥ 1	0.310	84	0.279	61	0.6660
Cusp 7	ldm2	≥ 1	0.506	85	0.540	63	0.6707
Protostylid	ldm2	≥ 2	0.203	80	0.400	56	0.0255*
Deflecting wr	ldm2	≥ 1	0.278	72	0.340	53	0.4239

Notes:
* The p-value is significant at the 0.05 level.
** Fisher's exact test.

18.3 Results

Trait frequencies, chi-square probabilities, and, where appropriate, Fisher's exact test results, are presented by sex in Table 18.2. Three of the twenty-two traits (13.6 percent) exhibited significant sex differences in frequency: udi2 shovel shape, udm2 Carabelli's trait, and ldm2 protostylid. The results constitute a low level of sex dimorphism, consistent with reduced dimorphism typically observed in morphometric features of the deciduous versus permanent dentition. The inability to determine sex accurately in immature archaeologically derived skeletal remains and the need to use sex-pooled data in comparative analyses led us to pool data for all morphological traits in this study.

Table 18.3. *Expression of nonmetric traits in maxillary teeth*

Crown trait/complex			Grade of trait expression [n individuals (%)]				
Shovel shape	Tooth	n	0	1	2	3	
(Hanihara 1961)	di1	129	60 (46.5)	60 (46.5)	9 (7.0)	–	–
	di2	131	16 (12.2)	75 (57.3)	40 (30.5)	–	–
	dc	140	40 (28.5)	74 (52.9)	26 (18.6)	–	–
Tuberculum dentale	dc		0	1	2	–	–
(Turner et al. 1991)		140	97 (69.3)	35 (25.0)	8 (5.7)	–	–
Conical crown	dc		0	1	–	–	–
(see text)		132	132 (95.0)	7 (5.0)	–	–	–
Talon cusp	di2		0	1 (full)	2 (semi)	3 (trace)	–
(Hattab et al. 1996)		148	145 (98.0)	1 (0.6)	2 (1.4)	–	–
Paramolar tubercle	dm1		0	1 (ridge)	–	3 (cusp)	–
(Jørgensen 1956)		148	83 (56.1)	60 (40.5)	–	5 (3.4)	–
Cusp number	dm1		2	3M (1 &2)	3H (1&2)	4 (4- & 4)	–
(Hanihara 1961)		140	37 (26.4)	52 (37.1)	22 (15.7)	29 (20.7)	–
Hypocone size	dm2		3+A	3+B	4-	4	–
(Hanihara 1961)		140	0 (0.0)	0 (0.0)	24 (17.1)	116 (82.7)	–
Carabelli's trait	dm2		0	1 (pit/grv)	2 (Y)	3 (welt)	4 (cusp)
(Grine 1986)		140	31 (21.1)	60 (40.8)	27 (18.4)	9 (6.1)	20 (13.6)
Cusp 5 (metaconule)	dm2		0	1	2	3	–
(Turner et al. 1991)		145	134 (92.4)	7 (4.8)	4 (2.8)	0 (0.0)	–

Initially we present trait frequencies for crown morphology and then address two specific issues in the comparative analysis: (1) biological affinities of the Javanese sample are assessed to determine their relationship with other living and prehistoric groups, and (2) whether the Javanese deciduous dental pattern can be considered "Sundadont," a pattern initially recognized and defined for nonmetric traits of the permanent dentition.

18.3.1 Malay deciduous tooth crown morphology: trait frequencies

Crown trait frequencies for maxillary and mandibular teeth are presented in Tables 18.3 and 18.4, respectively. In the maxilla, traits infrequently observed include conical canine crown shape (5.0 percent), full and semi talon cusp (2.0 percent), cuspal expressions (Jørgensen 1956, type b) of the parastyle (or paramolar tubercle; 3.4 percent), and delta-shaped ldm1 (6.5 percent; Figure 18.2). Shoveling is weakly expressed; full expressions of shovel shape (grade 3) were not observed. Cusp number of the udm1 and udm2 Carabelli's trait are the most polymorphic variants, with 3M (1 & 2). the most frequent cusp variant, while pits and grooves were the most commonly expressed Carabelli's form (Figure 18.3).

Table 18.4. *Expression of nonmetric traits in mandibular teeth*

Crown trait/complex	Tooth n	Grade of trait expression – n individuals (%)				
Winging	di1	1	2	3	4	5
(Enoki and Dahlberg 1958)	105	34 (32.4)	16 (15.2)	53 (50.5)	2 (1.9)	0 (0.0)
Conical crown shape	dc	0	1	–	–	–
(see text)	139	137 (98.6)	2 (1.4)	–	–	–
Shovel shape	di-dc	0	1	2	–	–
(Hanihara 1961)	137	89 (65.0)	43 (31.4)	5 (3.7)	–	–
Delta-shaped crown	dm1	0	1	–	–	–
(Hanihara 1961)	139	130 (93.5)	9 (6.5)	–	–-	–
Cusp number	dm1	4	5	6	–	
(Hanihara 1961)	139	46 (33.1)	88 (63.3)	5 (3.6)	–	
Groove pattern	dm2	Y	+	X	–	–
(Turner et al. 1991)	97	92 (94.8)	3 (3.1)	2 (2.1)	–	–
Hypoconulid size – C-5	dm2	2	3	4	5	n
(Turner et al. 1991)	139	4 (2.9)	17 (12.2)	78 (56.1)	40 (28.8)	–
Entoconulid size – C-6	dm2	0	1	2	=> 3	–
(Hanihara 1961)	145	102 (70.3)	6 (4.1)	25 (17.2)	12 (8.3)	–
Metaconulid size – C-7	dm2	0	1	2	=>3	–
(Hanihara 1961)	148	71 (48.0)	73 (49.3)	3 (2.7)	0 (0.0)	–
Deflecting wrinkle	dm2	0	1	2	–	–
(Hanihara 1961)	127	88 (69.3)	38 (29.9)	1 (0.8)	–	–
Protostylid	dm2	0	1	2	3	=> 4
(Hanihara 1961)	136	73 (53.7)	24 (17.9)	12 (9.0)	19 (14.0)	8 (5.9)

Full expressions of the hypocone predominate and greatly reduced forms (3+A and 3+B) were not observed. While present in 7.6 percent of the sample, expressions of cusp 5 were small in size (grades 1 & 2).

Variable expressions of incisor winging are typically observed in permanent UI1s (Enoki and Dahlberg 1958), but polymorphic variation in winging was prevalent in the ldi1s of this sample. While straight alignment (grade 3) was most common, bilateral winging was the next most frequently expressed variation (grade 1, 32.4 percent). Conical canine crown shape is less frequent in mandibular canines (1.4 percent) than in maxillary canines (5.0 percent). Shovel shape of lower canines and incisors is infrequent and only weak expressions (grades 1 & 2) were observed. The ldm1s exhibited delta (or triangular) shaped crowns with moderate frequency (6.5 percent) and were predominantly five-cusped (63.3 percent). The Y-groove pattern of the ldm2 (95%) was dominant over alternative variants (+ and x). The hypoconulid (cusp 5) was always present and large in size, with grades 4 and 5 observed in 85 percent of the sample. The entoconulid (29.7 percent) was less frequent

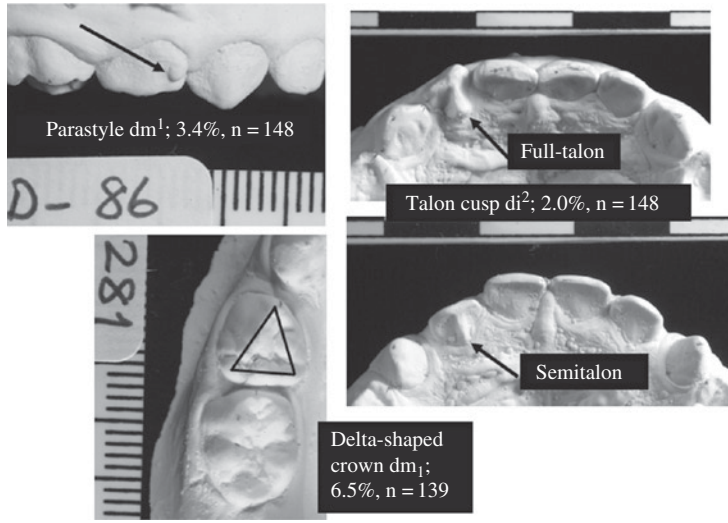
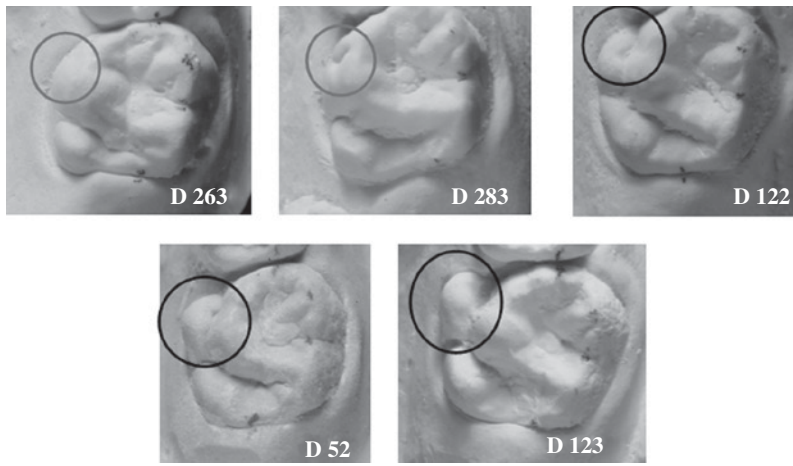


Figure 18.2. Rare morphological variants: talon cusp (udi2), parastyle (udm1), delta-shaped crown (ldm1).



Variation in expression of maxillary molar traits:
Carabelli's trait (circled) and Hypocone size

Figure 18.3. Variation in expression of maxillary molar traits: Carabelli's trait and hypocone size.

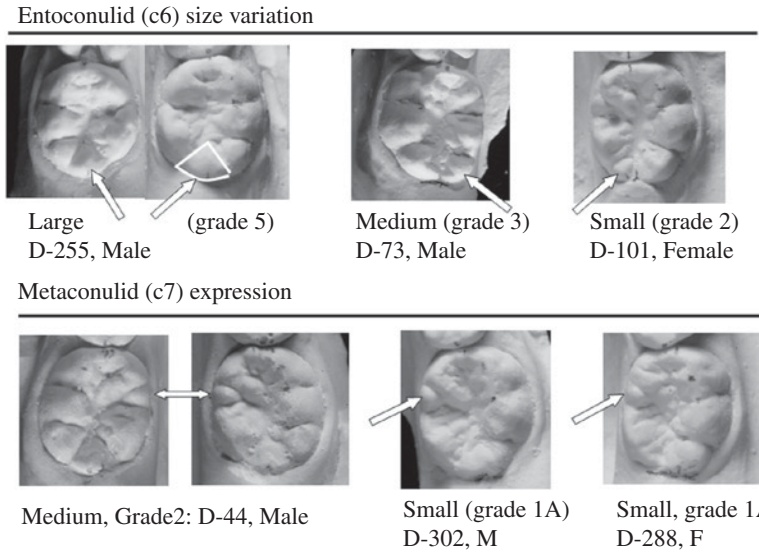


Figure 18.4. Expression of mandibular accessory cusps: C-6 (entoconulid) and C-7 (metaconulid).

than the metaconulid (52 percent) but included fuller expressions (≥ grade 3) in 8.3 percent of the sample (Figure 18.4). By contrast, the metaconulid typically exhibited small sizes (grades 1 & 2) and no variants of grade 3 or greater were observed. Expression of the deflecting wrinkle was infrequent, but the protostylid exhibited a wide range of expression.

18.3.2 Biological affinities from deciduous dental morphology: prehistoric and modern samples

In this section we assess biological relatedness of the Javanese deciduous dental sample with prehistoric and living samples from Asia, Old World, and global settings. Two different groups of comparative samples and two multivariate methods of estimating biological distance are used. Dental trait frequencies for each comparison are presented in Tables 18.5 and 18.6. Standardized trait frequencies were used in calculating measures of biological distance; results are presented graphically (Figures 18.5 and 18.6). In the cluster analysis distance was assessed using Ward's minimum-variance method, in which the distance between two clusters is the ANOVA sum of squares between the two clusters summed over all variables (Ward 1963; SAS Institute, Inc.). Ward's technique

Table 18.5. *Trait frequency data for prehistoric (in bold) and modern samples*

Group	Malay		Japan		**Jomon**		AmW		AmB	
Trait[a]	f	n	f	n	f	n	f	n	f	n
shv_udi2	0.305	131	0.878	41	0.476	21	0.000	24	0.095	21
cno_udm1	0.207	140	0.297	37	0.279	43	0.000	55	0.200	50
hyp4_udm2	0.827	140	0.730	89	0.854	48	0.737	57	0.902	51
cara_udm2	0.297	140	0.115	104	0.111	45	0.357	56	0.118	51
shv_ldc	0.036	137	0.055	199	0.088	34	0.020	49	0.021	47
c6_ldm2	0.297	145	0.333	45	0.607	56	0.073	55	0.140	50
c7_ldm2	0.514	148	0.870	46	0.680	50	0.407	54	0.468	47
proto_dm2	0.287	136	0.538	52	0.432	44	0.145	55	0.170	47
Group	SAfB		KalSan		**NNA**		**INM**		–	
Trait	f	n	f	n	f	n	f	n	–	–
shv_udi2	0.000	27	0.115	52	0.925	147	0.308	26	–	–
cno_udm1	0.314	35	0.562	73	0.495	188	0.114	44	–	–
hyp4_udm2	0.943	35	0.879	99	0.995	222	0.652	46	–	–
cara_udm2	0.031	32	0.084	95	0.226	217	0.088	45	–	–
shv_ldc	0.000	37	0.013	75	0.439	150	0.029	35	–	–
c6_ldm2	0.184	39	0.333	69	0.474	230	0.180	61	–	–
c7_ldm2	0.539	38	0.408	76	0.474	230	0.017	60	–	–
proto_dm2	0.162	47	0.065	93	0.283	233	0.016	61	–	–

Notes: Sample data sources and key to abbreviations: Malay (this study); Japan and Jomon (Kitagawa 2000); AmW – American White and AmB– American Black (Hanihara 1968); SAfB – South African Black (Grine 1986); KalSan –Kalahari San (Grine 1990); NNA – Native North American (Sciulli 1998); INM — Inamgaon (Lukacs and Walimbe 1984).

[a] Trait abbreviations and breakpoints: shv_udi2 – shovel shape, upper lateral incisor (presence = grades 2–3) cno_dm1 – cusp number, first upper molar (-4, 4) hyp4_udm2 – hypocone development, upper second molar (4) cara_udm2 – Carabelli's trait, upper second molar (4–7) shv_ldc – shovel shape, lower canine (2–3) c6_ldm2 – cusp 6, entoconulid, lower second molar (≥ 1) c7_ldm2 –cusp 7, metaconulid, lower second molar (≥ 1) proto_ldm2 – protostylid – lower second molar (≥ 2).

is widely used in anthropological biodistance studies; it is hierarchical and agglomerative and reliably yields clusters that accurately represent known group relationships (Ward 1963). The primary value of correspondence analysis is that it provides a simultaneous graphic display of traits and groups, enabling the investigator to visualize which traits are contributing to intersample variation (SAS Institute, Inc.) (Figure 18.6).

The first comparison used Ward's method to determine the affinities of nine groups: six represent contemporary living groups (American White; American Black; Japanese; Kalahari San; South African Black; and Javanese/

Table 18.6. *Trait frequencies for correspondence analysis (eight groups; six traits)*

Group	Japan		AmW		AmB		SAfB		KSan		Malay		Pima		Eskimo	
Trait	f	n	f	n	f	n	f	n	f	n	f	n	f	n	f	n
shv_udi1	0.766	124	0.000	20	0.100	10	0.000	20	0.043	47	0.070	129	0.615	78	0.500	16
hyp4_udm2	0.707	191	0.737	57	0.902	51	0.943	35	0.879	99	0.827	140	0.824	?	0.745	?
cara_udm2	0.125	185	0.357	56	0.118	51	0.031	32	0.084	95	0.207	140	0.000	118	0.000	?
c6_ldm2	0.333	45	0.073	55	0.140	50	0.184	38	0.333	69	0.297	145	0.368	117	0.377	53
c7_ldm2	0.87	46	0.407	54	0.468	47	0.538	39	0.408	76	0.514	148	0.729	118	0.794	63
proto_ldm2	0.447	152	0.145	55	0.170	47	0.162	37	0.065	93	0.284	136	0.890	118	0.673	52

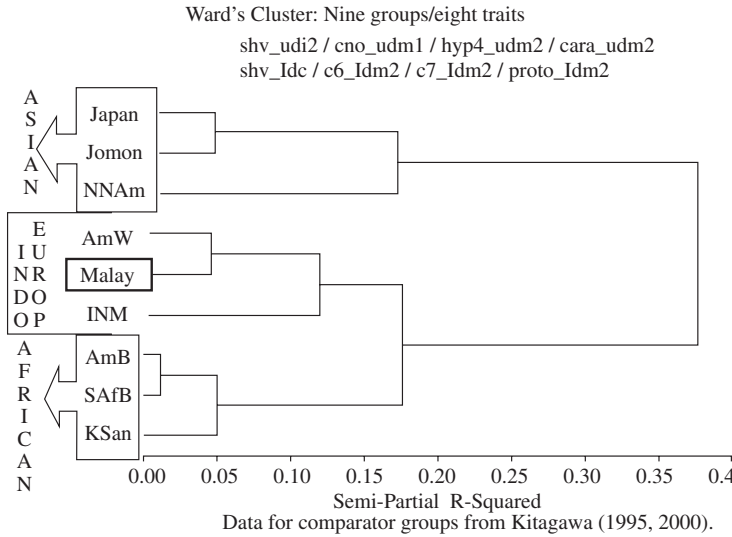


Figure 18.5. Cluster analysis of nine prehistoric and modern groups using Ward's minimum-variance method and eight nonmetric tooth crown traits.

Malay – this study), while three represent prehistoric, archaeologically derived samples (Inamgon; Jomon; Native North American). Eight nonmetric traits were used (shovel shape – udi2; cusp number – udm1; hypocone size – udm2; Carabelli's trait – udm2; shovel shape – ldc; hypoconulid (c6), entoconulid (c7), and protostylid – ldm2). This comparison includes a mix of living and prehistoric samples and uses data and trait breakpoints from Kitagawa and colleagues (1995; Kitagawa 2000). Frequency data are presented in Table 18.5.

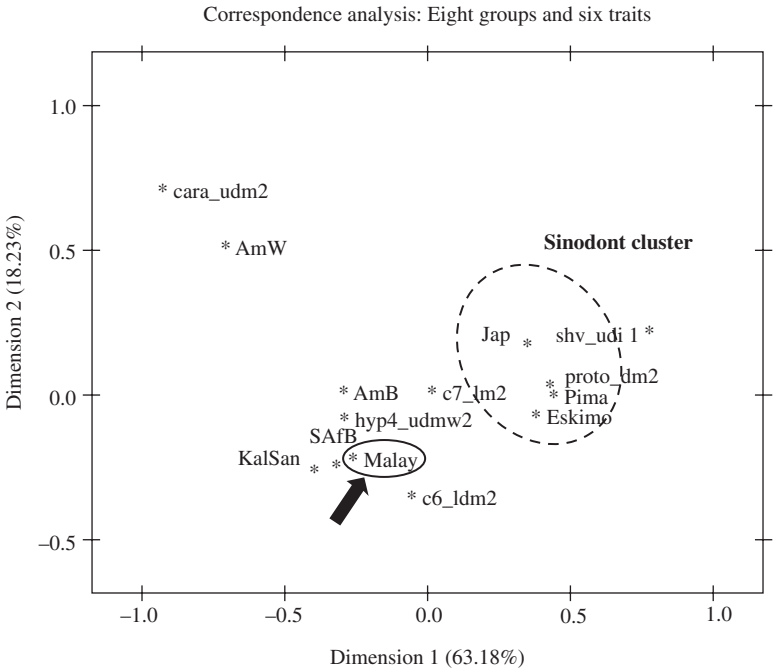


Figure 18.6. Correspondence analysis of eight groups using six nonmetric tooth crown traits.

Results of the first comparison (Figure 18.5) produced three distinct clusters, including (1) an Asian cluster consisting of modern Japanese, prehistoric Jomon, and Native North Americans; (2) an Indo-European cluster composed of American White and the Javanese Malay sample, and the prehistoric sample from western India – Inamgaon; and (3) an African cluster, containing American and South African Black groups, and Kalahari San.

The second assessment of biological affinity used correspondence analysis to assess affinities among eight groups: three African or African-derived (South African Black; Kalahari San; American Black), one European or European-derived (American White), one Asian (Japanese), two Native North American (Eskimo and Pima), and the Javanese/Malay (this study). Six traits were used (shovel shape – udi1; hypocone size and Carabelli's trait – udm2; hypoconulid (c6), entoconulid (c7), and protostylid – ldm2). Frequency data are presented in Table 18.6. Comparative data and breakpoints are from Kitagawa and colleagues (1995). The first two dimensions explain 81.4 percent of the variation (Figure 18.6) and reveal a distinct

Sinodont cluster (Japanese, Eskimo, and Pima) to the right. Shovel shape (udi1) and protostylid (ldm2) contribute to the distinctive identity of this group. The American White sample is in the upper left quadrant of the plot and the frequency of Carabelli's trait contributes to its divergent position. The Javanese Malay sample clusters with African (South African Black, Kalahari San) and African-derived (Afro-American Black) samples in the lower middle section of the plot, "pulled" in that direction by hypocone size (udm2) and hypoconulid frequency (ldm2).

18.4 Discussion

Deciduous crowns present an array of nonmetric traits, 22 of which were included in this study. We documented trait frequencies and the range of trait expression in this sample of Javanese schoolchildren, then assessed relative biological affinity with living and prehistoric Asian and global samples. These new data on variation in Javanese deciduous dental morphology permit further discussion of biological affinities and allow us to address questions of anthropological interest, including (1) are Javanese biological affinities closer to the African, East Asian, or the Indo-European deciduous dental pattern? and (2) can the Javanese Malay deciduous dental trait complex be labeled Sundadont?

18.4.1 Are Javanese biological affinities closer to African, Asian, or Indo-European groups?

The outcome of biological divergence analyses depends heavily on the selection of nonmetric traits by investigators and their choice of groups. Other investigators have called attention to this limiting factor in comparative studies of deciduous morphology (Kitagawa 1995) because it imposes severe restrictions on the number of variables and/or groups. Despite these limitations, both comparative analyses, that is, the cluster and the correspondence methods, yielded consistent results; Javanese Malay did not exhibit close affinities to any of the Sinodont groups (Japanese, Eskimo, or Pima). However, the two comparative analyses did yield different patterns of group affiliation. Results of the first comparison found the Javanese sample clustering with the late prehistoric–protohistoric sample from Inamgaon, western India (1100–700 BC), and a modern European-derived sample. This result is consistent with the hypothesis that Javanese dental morphology reflects the impact of "late arriving"

migrants or relatively recent gene flow from the northwest (e.g., Indian subcontinent). Archaeological and historical evidence indicates that many aspects of Indonesian culture, including art, architecture, dance, religion, and social organization, have been strongly influenced by antecedents whose distinctive features originate in the peoples and cultures of the Indian subcontinent (Mullick 1986–1987; Sedyawati 1982). It may not be surprising that the evidence from deciduous dental morphology suggests biological influences from India as well.

By contrast, correspondence analysis resulted in the Javanese/Malay sample grouping with African and African-derived groups (American Blacks). This result appears contradictory to that of the cluster analysis yet is consistent with arguments for a southern coastal dispersal out of Africa into insular Southeast Asia and Australia (Endicott et al. 2007; Mellars 2006; Stringer 2000). If the Javanese deciduous dental sample has an ancestral heritage that includes earlier input from an out of Africa dispersal event, then the clustering of Javanese with African groups may be suggestive of this deeper ancestry. This result is consistent with results of a global analysis of biological affinities among 21 regional groups based on 23 polymorphic nonmetric traits of the permanent dentition (Scott and Turner 1997:288). In their analysis, the Sunda- and Sahul-Pacific groups, including prehistoric and recent Southeast Asian samples, clustered more closely with sub-Saharan Africans than with other East (Jomon) and North (Siberian) Asian groups.

Larger and more diverse – geographically and chronologically – dental samples might provide the frequency data required to confirm or reject potential affinities with African and African-derived or Indo-European groups. Alternatively, ethnic Malay may exhibit heterogeneity in their biological ancestry as inferred from deciduous dental morphology – with some groups showing closer affinities to African samples, while others may have derived a greater proportion of their ancestral heritage from southern Asians. Documentation of deciduous nonmetric traits in Malay from other locations in and around Java is required to clarify these issues.

A primary focus of regional archaeological, genetic, and linguistic research is dedicated to reconstructing the route and timing of migration into the Pacific Islands from China, Taiwan, and eastern Indonesia (Cox et al. 2005; Hill et al. 2007). Less research has been devoted to identifying the origins of western Indonesian populations such as the Javanese Malay. Consequently the results of our biodistance analyses contribute a new perspective on Southeast Asian population relationships. Our results suggest that Northeast Asians are an unlikely ancestral source for the Malay sample, but that currently available data are insufficient to choose between African

and South Asian source populations. It is entirely possible that Javanese heritage may involve variable levels of genetic input from both African and South Asian populations.

18.4.2 Is the Javanese/Malay deciduous dental complex Sundadont?

The "Mongoloid dental complex" in deciduous teeth was initially described by Hanihara (1966) following the earlier recognition of this pattern in permanent teeth by Tratman (1950) and subsequently further developed by Hanihara (1968). This complex of the permanent dentition was later subdivided into a northern, derived, and morphologically complicated Sinodont pattern contra a southern, morphologically simpler pattern labeled Sundadont (Turner 1990). The original characterization of Sundadonty was based on relative frequency differences in eight nonmetric traits of permanent teeth in Southeast Asians versus Northeast Asians and Native North Americans (Sinodonts; Turner 1990). These traits include UI1 shovel shape, UI2 double shovel, single-rooted UP1, UM1 enamel extension, UM3 peg-reduced-congenital absence, LM1 deflecting wrinkle, three-rooted LM1, and four-cusped LM2. Mean frequencies are significantly lower in Sundadonts than Sinodonts for the first seven traits, and significantly greater for the last.

The question of whether a Sundadont dental pattern is present in deciduous nonmetric traits has been raised, but not fully answered, by Kitagawa and colleagues (1995; Kitagawa 2000). We believe it is significant that neither of our analyses (using cluster or correspondence methods) based on deciduous nonmetric traits showed linkage with Sinodont groups (Eskimo, Japanese, or Pima). However, three obstacles render recognition of Sundadonty in the deciduous dentition of Javanese Malay tenuous: (1) the study was conducted on casts, not archaeologically derived or recent skeletal samples; (2) some nonmetric traits appear to exhibit different modes of expression in deciduous versus permanent teeth (Edgar and Lease 2007; Kitagawa et al. 2000); and (3) all relevant nonmetric traits are not systematically scored and recorded by all morphologists (Kitagawa et al. 1995).

18.4.2.1 Dental casts versus real teeth

Three of eight traits defining the Sundadont dental complex (single-rooted UP1, UM1 enamel extensions, and three-rooted LM1) cannot be observed in dental casts. One trait has no direct parallel in the deciduous dentition (peg-reduced-congenital absence of the UM3). Another is not typically observed in studies of deciduous dentition (UI1 double shovel) because of its rarity. Thus,

only three features of Sundadonty can be comparatively assessed in deciduous dental casts: udi1 shoveling and deflecting wrinkle and cusp number – both in the ldm2.

18.4.2.2 Differences in trait expression in permanent and deciduous teeth

Discordant results have been reported in estimating intergroup biological distance from deciduous and independently from permanent dental morphology. Such analyses have been conducted on U.S. Amerindian groups (Nelson and Griffin 1996), a European-derived American sample (Edgar and Lease 2007), and prehistoric and living East Asian samples (Kitagawa et al. 1995; Kitagawa 2000). Nelson and Griffin (1996) list three factors accounting for these discrepancies: (1) use of different traits in deciduous and permanent teeth, (2) composition of subadult and adult samples representing different subgroups of the population, and (3) independent development of deciduous and permanent dentitions. For example, distinctive modes of expression of the metaconulid in ldm2 and LM1 yield contrastingly high trait frequencies for c7 in ldm2 and relatively low frequencies for C7 in LM1 in immigrant Yayoi and post-Yayoi Japanese (Kitagawa 2000: 250).

18.4.2.3 All relevant morphological traits not scored

Dental morphologists do not consistently list the same nonmetric traits for observation in their analyses. Factors responsible for variability in trait lists may include ease of recognition, consistency in classification, resistance to eradication by tooth wear, and relevance to the research problem. For, example, in discussing trait differences between East Asian Sinodonts (Immigrant Yayoi and post-Yayoi Japanese) and Sundadonts (Jomon and Tanegashima Yayoi), Kitagawa (2000) noted inconsistency in scoring and reporting frequencies of the distal and middle trigonid crests, precluding intergroup comparison for these traits. Comparison of nonmetric frequency data derived from casts and real skeletal specimens limits the number of direct comparisons that can be made and reduces the pool of samples available for comparative analysis of intergroup biodistance.

Though complicated by several of the issues discussed previously, the Jomon deciduous dental pattern has been characterized as Sundadont (Kitagawa 2000), a trait complex typically described by frequent expression of morphologically simple traits. Though disparities exist in the size of Javanese Malay and Jomon samples, a comparison of eight trait frequencies (see Table 18.5) reveals that five are not significantly different [lateral incisor shovel shape-udi2 ($p = 0.12$);

cusp number-udm1 (p = 0.32); hypocone size-udm2 (p = 0.68); lower canine shovel shape-ldc (p = 0.20); and protostylid-ldm2 (p = 0.13)]. By contrast, three traits show significant differences: Carabelli's trait-udm2 is more frequent in Javanese Malay (p = 0.01), while c6 – the entoconulid ($p < 0.01$) – and c7 – the metaconulid ($p = 0.0405$) – are significantly less frequent in the Javanese sample. These results suggest that the Javanese Malay exhibit some key components of the Sundadont complex (low expression and frequency of udi and ldc shoveling, similarities in udm1 cusp number, udm2 hypocone size), but also display differences from the standard expression of Sundadonty. For example, accessory cusps of ldm2s (c6, c7) are rarer, and Carabelli's trait of the udm2 are more common, than expected. These differences can be interpreted to suggest that the Javanese Malay deciduous dentition is not precisely equivalent to Sundadonty as expressed in the permanent dentition. Difference are due to (1) simplification of lower molar morphology (low frequencies of c6 and c7) and simultaneously (2) to increased complexity in upper molar morphology (higher frequency of Carabelli's trait). The latter distinction may reflect recent gene flow, or population movement, into Indonesia from Indo-European groups of South Asia. These observations and the absence of an affiliation between the Javanese/Malay sample and Sinodonts in our analyses, suggest that the Javanese deciduous pattern may be appropriately, yet preliminarily, labeled Sundadont.

18.5 Conclusions

This analysis of the crown morphology of Javanese deciduous teeth provides the first full characterization of nonmetric trait expression, variability, and frequency for insular Southeast Asia. These data reveal the presence of certain rare, yet interesting traits, including the talon cusp (udi2; 2.0 percent, n = 148), conical canine crown (udc; 5.0 percent, n = 132), parastyle (udm1; 3.4 percent, n = 148), and delta-shaped ldm1 (6.5 percent, n = 139). Although udi1s consistently exhibited straight alignment, we found consistent patterns of bilateral winging of ldi1s (32.4 percent; n = 105), a trait not commonly reported.

This Javanese sample presents simplified crown morphology, in which the expression of five traits is consistent with the Sundadont pattern. The trait complex can be described as having low frequencies of udi1 shoveling, udm2 metaconule (c5), and ldm2 accessory cusps (c6, c7). Commonly occurring variants included Carabelli's trait (udm2; 78.9 percent, n = 140), which included welt and full cuspal expressions, and large hypocone size (grade 4; 82.7 percent,

n = 140). Different comparative samples and distance statistics yielded two main patterns of biological relationship: (1) in the cluster analysis Javanese clustered closely with Indo-European samples including those from prehistoric India and Europe, while (2) in the correspondence analysis the Javanese grouped with African and African-derived samples. We regard these alternate outcomes as consistent with different hypothesized migration scenarios and population histories. Further research on nonmetric traits of the deciduous dentition that includes additional samples of Malay from western Indonesia and samples from mainland South and East Asia is essential to determine Malay biological affinities more precisely.

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Appendix: Crown trait definitions and classifications

Twenty-two tooth trait combinations were included in the analysis: 11 maxillary and 11 mandibular. We define these traits, describe scoring and classification of trait variation, and provide reference to key sources on which

the trait descriptions, scoring methods, and categories of classification are described here.

Maxillary crown traits

Shovel-shape (udi1, udi2, udc). Variation in prominence of the mesial and distal marginal ridges of the lingual surface of the tooth crown were observed. The four scale system of classification advocated by Hanihara (1961) for deciduous maxillary incisor teeth was used (0 = absent, 1 = slight or trace shovel, 2 = moderate, and 3 = marked). This system has been widely adopted in the investigation of maxillary incisor shoveling (Grine 1986, 1990; Kitagawa et al. 1995; Kitagawa 2000; Lukacs and Walimbe 1984; Sciulli 1990, 1998). Plaque D1 was used to classify variation in shoveling in central incisor teeth and Plaque D2 to evaluate lateral incisors and canine teeth.

Talon cusp (udi1, udi2). The labial and lingual surfaces of maxillary and mandibular incisor teeth were observed for evidence of talon cusp development. A talon cusp is a morphologically well-delineated cusp or prominent ridge that projects from the lingual or labial surface of maxillary or mandibular primary or permanent anterior teeth and extends at least half the distance from the cementoenamel junction (cingulum) to the incisal edge of the tooth (Chin-Ying et al. 2001; Lukacs and Kuswandari 2008). Variation in trait expression and criteria for classification follow (Hattab et al. 1996; Hattab and Yassin 1996). Three categories are recognized: type 1 (Talon) – a morphologically well-defined additional cusp extending at least half the distance to the incisal edge; type 2 (Semitalon) – an additional cusp projecting from the lingual fossa, more than a millimeter, that extends from the cingulum less than half the distance to the incisal edge; type 3 (Trace talon) – enlarged or prominent cingula and their variations.

Tuberculum dentale (udc). The development of the lingual cingulum of the maxillary canine was observed and the amount of projection was scored from 0 = smooth surface, no cinguluar development; to 1 = slight projection; 2 = moderate projection; 3 = tubercle with free cuspal apex. The number of ridges was not scored, only the degree of projection of the cingulum. This represents a modification of Grine's (1986) classification of the tuberculum dentale.

Conical crown shape (udc). Shape of the maxillary canine tooth crown was observed and scored as either "normal" or "conical." Normal maxillary deciduous canine crowns are characterized by buccolingual compression and

mesiodistal elongation and the greatest mesiodistal diameter of the maxillary canine crown is at midcrown height or approximately midway between the cervix and the apex of the crown. By contrast, conical canines exhibit an anomalous shape that is approximately "circular" in occlusal view, "conical" when viewed from a labial or buccal perspective, and the greatest crown dimensions are at the base of the crown – at the gingiva (Figure 18.2, uldc in "semitalon" specimen).

Paramolar tubercle (udm1). Morphological variation on the buccal surface of maxillary first deciduous molar teeth extends from the eminence forming the mesiogingival cingulum. Jørgensøn (1956) described the trait and classified expression into two categories: (a) in which the eminence is limited occlusally and distally by a rounded groove, and the tip is not free and (b) in which the eminence is strongly developed and the tip is free [e.g., the tip extends higher occlusally than the furrow by which it is separated from the buccal surface (Jørgensen 1956)]. We adhere to established terminology in which the labels "welt" and "cusp" are used for Jorgensøn's categories (a) and (b), respectively (Grine 1986; Kitagawa et al. 1995; Kitagawa 2000).

Cusp number (udm1). Variation in number and size of cusps on the occlusal surface of deciduous first maxillary molar teeth may range between two and four. Hanihara (1961) subdivided the expression of cuspal patterns into seven categories (2, 3M1, 3M2, 3H1, 3H2, 4-, and 4) based primarily on the presence of two, three, or four cusps. Cuspal variation was initially sorted into these categories using Hanihara's Plaque D5, but some categories were merged for data presentation and comparative analysis. The following four categories are used:

2:	two cusps are present – protocone and paracone
3M (1 & 2):	three cusps are present – protocone, paracone, and metacone. Variations in metacone size [small (M1), large (M2)] are combined.
3H (1 & 2):	three cusps are present – protocone, paracone, and hypocone. Variations in hypocone size [small (H1), large (H2)] are combined.
4 (4- & 4):	four cusps are present – protocone, paracone, metacone, and hypocone. Variations in size and juncture of the metacone and hypocone [small (4-), large (4)] are combined.

This concatenation of subcategories facilitates comparability of results with data from other investigators.

Cusp number/hypocone variation (udm2). The number and size of cusps on the occlusal surface of the second deciduous maxillary molar were classi-

fied by Hanihara (1961) into five categories as illustrated in Plaque D6. These categories include:

3:	three cusps are present – protocone, paracone, and metacone; the hypocone is absent. This form of cuspal expression has not been observed in deciduous second maxillary molars (Hanihara 1961).
3+A:	three main cusps are present plus a small hypocone distolingually. This expression is equivalent to the grade 3+ in Dahlberg's (1951) system of classification for permanent maxillary molars (Dahlberg 1951).
3+B:	three main cusps are present plus a small hypocone distolingually. This form is distinguished from 3+A by a groove demarcating hypocone:metacone contact on the distal margin of the crown.
4-:	three primary cusps plus a hypocone of "small" size that is connected to the metacone without interruption by a groove.
4:	four main cusps are well developed and the hypocone is fully expressed.

Data were collected using the grades described. Established practice was followed in summary presentation of data and comparative analyses, in which grades 4- and 4 were combined (Kitagawa et al. 1995; Kitagawa 2000; Sciulli 1998).

Carabelli's trait (udm2). A variety of anatomical features, including pits, grooves, welts, bulges, and cusps, are regularly expressed on the (mesio)lingual surface of the protocone in maxillary molar teeth. A "bewildering array of classificatory schemes" (Grine 1986) has been developed to systematize scoring of variation in this trait, yet most recognize a few key forms of expression: pits, grooves (fissures), welts, and cusps. Both the Arizona State University Dental Anthropology System for scoring morphological traits in maxillary permanent molars (Turner et al. 1991; Scott and Turner 1997) and the Hanihara (1961) system (Plaque D7) for deciduous maxillary molars both advocate classification into eight categories. By contrast, only four categories are used in Grine's (1986) system. A comparison of these systems is provided in Table 18.7 for ease of reference and identification of concordances. Data were collected using a descriptive hybrid system that recognized pits, single and double vertical grooves, small and large Y-shaped grooves, and cusps of small, medium, and large size. Individual investigators' preferences vary, with some – such as Sciulli (1998) – preferring Grine's (1986) system, while Kitagawa and colleagues (1995, 2000) adopted Hanihara's (1961) system. Here we follow Kitagawa's (1995) equivalence in which Hanihara's cuspal categories (grades 4 through 7) are regarded as synonymous with Grine's (1986) grades III and IV.

Cusp 5/metaconule (udm2). In this analysis the metaconule, or cusp 5, of maxillary molar teeth is an accessory cusp located on the distal marginal ridge between the metacone and the hypocone. Displaying closer linkage to the

Table 18.7. *Classification of Carabelli's trait in deciduous and permanent teeth*

Hanihara (1961, 1963)		Grine (1986)		Turner et al. (1991)	
Grade	Description	Grade	Description	Grade	Description
0	Absent	0	Absent	0	Absent
1	Shallow groove, trace pit	I	Pit or single vertical fissure	1	Groove
2	Shallow depression or groove	II	Fissure with horizontal limb or double vertical fissures	2	Pit
3	Depression or pit no groove or bulge	III	Fissures delimit swelling (welt) cervically	3	Small Y-shaped depression
4	Depression or pit with "eminence"	IV	Small to large cusps	4	Large Y-shaped depression
5	Strong eminence not encircled by groove	–	–	5	Small cusp, no free apex
6	Small cusp, eminence encircled by groove	–	–	6	Medium cusp, attached apex
7	Large cusp	–	–	7	Large free cusp

metacone, this cusp is demarcated on the disto-occlusal margin by buccal and lingual marginal grooves. The trait exhibits a broad range of variation in size and form that was divided into absent and five size grade categories of present by Harris and Bailit (1980). This system of classification has been widely adopted by students of permanent tooth crown morphology (Townsend et al. 1986; Scott and Turner 1997; Turner et al. 1991) and is used here in scoring the trait in deciduous maxillary molar teeth. This trait is different from the metaconule of Kitagawa and colleagues (1995; Kitagawa 2000), which is located on the crista obliqua linking the protocone and metacone (see Kitagawa et al. 2000: 245; Figure 18.2). The history, nomenclature, and related references for the metaconule, plagioconule, and cusp 5 in dental anthropology and primate paleontology are addressed by Grine (1986) and by Scott and Turner (1997).

Mandibular crown traits

Winging (right and left ldi1). Alignment of right and left deciduous mandibular central incisor teeth was viewed against a straight edge. Straight alignment and unilateral or bilateral rotation of central incisors, in the absence of dental

crowding, were scored according to the standard developed by Enoki and Dahlberg (Enoki and Dahlberg 1958) for permanent maxillary central incisors. This system recognizes five categories:

A: bilateral winging – distal margins of right and left central incisors are displaced labially, resulting in a broad V shape viewed occlusally.
B: unilateral winging – the distal margin of either the right or the left central incisor is displaced labially; the unrotated tooth retains straight alignment.
C: straight alignment – the incisal edges of right and left central incisor teeth form an undeviating straight line.
D: unilateral counterwinging – the distal margin of either the right or left central incisor is displaced lingually; the unrotated tooth remains in straight alignment.
E: bilateral counterwinging – the distal margins of both right and left central incisors are displaced lingually, resulting in a broad inverted V shape when viewed occlusally.

Shoveling (ldi1, ldi2, ldc). Mesial and distal marginal ridging of lower incisor and canine teeth was observed and classified collectively. Hanihara (1961) comments that shovel shape of lower incisors is too faint to be reliably classified into grades of expression as maxillary anterior teeth can. Plaque D4 was used to score lower canine shoveling and Plaque D2 designed for scoring shovel shape of maxillary lateral incisors was used to classify lower incisors. The greatest expression of shoveling in lower incisors or canines was recorded.

Conical crown shape (ldc). Shape of the mandibular canine tooth crown was observed and scored as either normal or conical, as described previously for maxillary canine teeth.

Cusp number (ldm1). This trait counts the number of primary cusps on the occlusal surface of the crown. Jørgensen (1956: 91) expressed concern over "diagnostic difficulties" in assessing cusp number in dm_1 due to variation in the presence and size of the hypoconulid. The criteria for recognizing and counting a cusp required apical distinction demarcated by fissures from adjacent cusps. No attempt was made to assess cusp size since comparatively few dental morphologists have recorded this variable in lower deciduous first molar teeth (Grine 1986).

Triangular (delta) crown shape (ldm1). This trait was initially recognized by Dahlberg (1949) and refers to the occlusal outline of the deciduous first mandibular molar. The common occlusal outline is trapezoidal. The alternate and rarer form results from a narrow trigonid and broad talonid and was designated triangular. Hanihara (1961) recognized and illustrated these two variants in Plaque D10, with type 1 being the common trapezoidal form and type

2 the triangular variant. Other workers have adopted the term "delta shape" (Kitagawa 2000) or "delta form" (Sciulli 1998) to refer to the "triangular" occlusal outline of Dahlberg (1949) and Hanihara (1961). We recorded dm_1 occlusal shape as either trapeziodal or triangular.

Cusp number and size (ldm2). Cusp arrangement and size variation in the deciduous mandibular second molar are homologous with cuspal variation in the permanent mandibular first molar. Some investigators recognize the dm_2 as the "polar tooth" in a morphogenetic field that extends through the first and second permanent molars to the third molar (Dahlberg 1951). Furthermore, though dental morphologists may not have systematically recorded deciduous molar cusp size prior to the mid-1980s (Grine 1986), more recent research includes scoring these variables (Kitagawa et al. 1995; Kitagawa 2000; Sciulli 2000). Consequently, we independently assessed groove form and relative size of three cusps – one primary cusp (the hypoconulid) and two accessory cuspules (the entoconulid and the metaconulid) – in the mandibular second deciduous molar.

Occlusal groove pattern (ldm2). The configuration of fissures on the occlusal surface of molars has often been scored in combination with cusp number. The four distinct categories recognized by (Hellman 1928; Y5, +5, Y4, and +4) were followed by many investigators. The Y5 or *Dryopithecus* occlusal pattern is a plesiomorphic hominoid attribute shared by humans and apes (Gregory and Hellman 1926). However, some researchers expressed concern that this scoring system linked traits (cusp number and groove form) whose expression may be independent. Today, cusp number is usually scored separately from groove form, and groove form is determined exclusively in the basis of cuspal contact (Jørgensen 1955). Three patterns were recognized in this classification: Y – with metaconid-hypoconid contact; + – in which all four cusps meet at a single point; and a new category, X – defined by protoconid-entoconid contact. Jørgensen's (1955) system was used in this analysis.

Hypoconulid/cusp-5 (ldm2); entoconulid/cusp-6 "tuberculum sextum" (ldm2); metaconulid/cusp-7/tuberculum intermedium (ldm3). Scoring the presence and size of these three cusps follows the procedure adopted by Sciulli (1998) for cusp 6 (tuberculum sextum) and cusp 7 (tuberculum intermedium) in which the classification recommended by Turner and colleagues (1991) for the hypoconulid, entoconulid, and metaconulid of permanent molar teeth is used to judge the relative size of c5, and accessory cuspules c6 and c7, in deciduous molars.

Deflecting wrinkle (ldm2). Uncommon in deciduous second lower molar teeth, the deflecting wrinkle is more frequently observed in permanent first mandibular molars of humans and great apes (Hanihara 1961; Grine 1986). In deciduous second mandibular molars a weakly or strongly developed metaconid ridge is straight and only rarely deflected, as in permanent molars. Grine

(1986) recommends four categories for trait classification of the central ridge of the metaconid: (1) absent, (2) weak and straight, (3) strong and straight, (4) deflected. In this study grades 3 and 4 were considered presence and grades 1 and 2 absence of the deflecting wrinkle.

Protostylid (ldm2). Defined as an elevation or ridge of enamel on the mesiobuccal surface of lower molars that extends from the gingival aspect of the buccal groove in a mesio-occlusal direction, the protostylid is classified into six categories (Dahlberg 1950; Hanihara 1961). The six categories depicted in Hanihara's (1961) Plaque D8 were used in this study.

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19 *Geographic structure of dental variation in the major human populations of the world*

TSUNEHIKO HANIHARA

19.1 Introduction

Research based on genetic and morphological data over the past 20 years has favored a replacement model for the origins of anatomically modern humans; under this scenario, our species can trace its genetic ancestry to a single origin in one or more African populations ca. 200,000 years ago (Cavalli-Sforza et al. 1994; Tattersall and Schwartz 2008), except for some possible genetic contributions from archaic humans (Abi-Rached et al. 2011; Green et al. 2010; Reich et al. 2010; Yotova et al. 2011). Relative to this dispersal, two major areas of concern are (1) possible expansion and colonization routes throughout the Eurasian continent and (2) the time scale(s) of colonization (Lahr 1996; Manica et al. 2005; Relethford 2004a).

Regarding routes from Africa to Eurasia, two major migratory pathways are presumed: the Levant corridor and the Horn of Africa (Cavalli-Sforza et al. 1994; Kivisild et al. 2004; Lahr 1996; Mellars 2006). The classic view, together with recent Y-chromosome analyses, emphasizes the Levant corridor, that is, the "northern route" (Luis et al. 2004; Underhill 2001). Several lines of recent genetic evidence suggest, on the other hand, a possibility for the Horn, or "southern route," that is, across the Bab el Madeb Strait along the Indian Ocean coastline (Chandrasekar et al. 2007; Forster and Matsumura 2005; Hudjashov et al. 2007; Macaulay et al. 2005; Oppenheimer 2003; Stringer 2000). One more possible route, the Strait of Gibraltar between Iberia and the Maghreb, apparently provided only a minor contribution to gene flow into Eurasia (Bosch et al. 2001).

Another interest in respect to prehistoric human dispersal is the peopling of East/Northeast Asia (reviewed by Hanihara and Ishida 2009). Genetic

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and morphological diversity and differentiation in eastern Asia have raised questions about the relationship between northern and southern populations (Cavalli-Sforza et al. 1994; Ding et al. 2000; Lahr 1996). Turner (1987, 1990, 1992) proposed the occupation of East/Northeast Asia resulted from a northward expansion of Southeast Asian peoples during the late Pleistocene. This model was recently reevaluated in many genetic studies (Ballinger et al. 1992; Disotell 1999; Li and Su 2000; Oppenheimer 2003; Shi et al. 2005; The HUGO Pan-Asian SNP Consortium 2009). On the other hand, several genetic and morphological studies suggest multiple migrations to East/Northeast Asia from western Eurasia, Central Asia, and South Siberia (Di and Sanchez-Mazas 2011; Hanihara 2006; Nakashima et al. 2010; Uinuk-Ool et al. 2003; Underhill et al. 2001; Wells 2002; Zhong et al. 2011).

It now appears that not only do sub-Saharan Africans have greater genetic and morphological diversity than other world populations (Cavalli-Sforza et al. 1994; Jorde et al. 2000; Mellars 2006; Relethford and Harpending 1994), but there is in addition a sequential decrease in diversity with distance from Africa – possibly due to iterative bottleneck effects during the process of expansion (Ayub et al. 2003; Cramon-Taubadel and Lycett 2008; Harpending and Rogers 2000; Hunley et al. 2009; Manica et al. 2005, 2007; Prugnolle et al. 2005; Ramachandran et al. 2005; Relethford 2004a, 2009, 2010). If so, the gradients of genetic and phenotypic diversity related to geography among major populations may address the process of occupation of the present range of modern peoples, including East/Northeast Asians.

Since the 1960s, many dental anthropologists have focused on crown and root traits for defining the dental characteristics of major geographic groups, and for reconstructing population history (K. Hanihara 1966, 1968; T. Hanihara 1992; Irish 1997, 1998; Mayhall et al. 1982; Scott and Turner 1997; Turner 1987). As Stojanowski and Schillaci (2006) emphasize, the primary benefits of morphological approaches are the availability of larger sample sizes, analytical efficiency, and the ability to include ancient populations. However, a morphological approach is essentially based on phenotypic similarity and therefore lacks testable underlying evolutionary models and taxonomic orientation. To examine the degree to which metric and nonmetric dental traits reflect underlying population structure and history that fit a neutral expectation, an R-matrix-based approach was adopted (Hanihara 2008, 2010a; Hanihara and Ishida 2005). Results suggest that dental morphological variation and diversification at the global scale are responsible for patterns of modern human emergence and dispersals; as such, it should be possible to test for population replacement versus *in situ* microevolution – both within and across geographic regions (Stojanowski and Schillaci 2006). Given this background, the purpose of this chapter is to explore possible migration and colonization routes across

Eurasia and, ultimately, to the New World and Oceania based on metric and nonmetric dental variation.

19.2 Materials and methods

Odontometric and nonmetric dental data sets from ten major geographic regions, totaling 7,807 male and 4,965 female adult specimens, were used. Brief sample information is provided in Table 19.1. Detailed information on country of origin, tribal affiliation, and cultural background is given elsewhere (Hanihara and Ishida 2005; Hanihara 2008).

To estimate quantitative dental parameters, mesiodistal and buccolingual crown diameters of all right teeth (up to 32 variables) were recorded in each specimen. When a right tooth was missing or damaged, the corresponding left tooth was measured. Measurements were taken according to the procedures of Hillson (1996). Only male specimens were used because of larger sample size. Morphological observations were made for 15 variables in the permanent dentition according to procedures in Table 19.2. The 15 traits include characteristics attributed to the eastern Asian/New World (Hanihara 1968), European (Mayhall et al. 1982), and sub-Saharan African dental complexes (Irish 1997, 1998), as well as key crown traits that distinguish Sundadonty from Sinodonty (Turner 1990). While observations were made for each side, the individual count method was used: if a trait was present on either or both sides, it was scored as present (Turner et al. 1991; Irish 2005). For the nonmetric data set, male and female data were combined since frequency distributions by sex are not significantly different in most samples, a strategy confirmed by Scott and Turner (1997).

In the present study, samples older than 2,000 years were excluded to preclude bias in the quality of the materials, with the exception of well-preserved Egyptian and Nubian samples. The dental series of Egypt and Nubia derive from predynastic through the Christian period and exhibit relative homogeneity (Irish 2005, 2006).

The degree of diversity within and between major geographic populations was estimated using an R-matrix approach. This method, originally developed for allelic frequency data, was modified for morphometric applications by Relethford and colleagues (Relethford and Blangero 1990; Relethford 1994, 1996, 2002; Relethford and Harpending 1994) and has been applied by many students since (González-José et al. 2003, 2005; Powell and Neves 1999; Roseman and Weaver 2004; Sardi et al. 2005; Schilaci and Stojanowski 2005; Scherer 2007; Steadman 2001; Stojanowski 2004). Recently, application of the R-matrix method has been extended to nonmetric phenotypic data (Hanihara

Table 19.1. *Materials used and brief information (parenthesis, number of individuals examined)*

Large geographic groups	Local groups	Brief information
1. East/Northeast Asia	Buryats (36)	Recent Buryats from Kiachta, Troiskosavsk (NMNH, AMNH, MH)
	Amur Basin (30)	Nivkhs, Ulch, Nanai, and other people, including a few specimens of Yakuts and Negidals (NHM, MH, AMNH)
	Mongol (224)	Recent Mongolians from Ulan Bator (AMNH, NMNH, MH)
	Japan (71)	Recent Japanese from Tokyo and Sapporo, collected by Kazuro Hanihara in 1960s (plaster cast) (UT)
	Northern China (66)	Recent Northeastern Chinese from Heilongjiang and Jirin Provinces (region formerly referred to as Manchuria) (UT, KU, AMNH)
	Southern China (63)	Recent Chinese from south of Cheng Kiang River (NHM, MH, AMNH)
	Tibet(77)	Recent Tibetans from Sikang and Kangting Provinces (NHM, UC, AMNH)
2. Southeast Asia	Vietnam (94)	Recent Vietnamese, mainly from Hanoi, including a few samples from Laos and Cambodia (MH)
	Thailand (61)	Recent Thai, mainly from Bangkok (AMNH, NHM, MH)
	Myanmar (130)	From Arracan Hills, Rangoon, etc. (NHM, CU)
	Malay (68)	Recent Malayans from Malay Peninsula, mainly from Singapore (AMNH, NHM, CU, FM)
	Andaman/ Nicobar Islands (109)	Recent inhabitants of the Andaman Island chain, Jarawa, and of the Nicobar Islands (NHM, UC, MH)
	Sumatra/Java (92)	Recent Sumatrans, including Nias, Banka, and other Islands, as well as Javanese, mainly from Jakarta (NHM, UC, MH, AMNH)
	Borneo (111)	Native inhabitants of Borneo Island, mainly the Land Dayaks (NHM, UC, MH, AMNH)
	Celebes/Molucca (50)	Recent inhabitants of the Celebes and Molucca Islands (NHM, UC)
	Lesser Sunda (28)	Recent inhabitants of the Lesser Sunda Islands – Timor, Bali, Sumbawa, and Flores Islands (NHM, UC, MH, AMNH)
	Philippines (173)	Recent Filipinos, Tagalog, Bilan, Bisaya, Irorot, Ifugao, and other tribes, mainly from from Luzon and Mindanao Islands (MHM, UC, MH, FM)

Table 19.1. (*cont.*)

Large geographic groups	Local groups	Brief information
	Negritos (55)	Recent Philippine Negritos, Aeta, and Agta from Luzon (UT, NHM, MH, AMNH, NMNH)
3. Australia	Northern Territory/ Queensland (48)	Recent Native Australians from Northern Territory and Queensland (AMNH, NMNH, UC)
	New South Wales/ Victoria (82)	Recent Australians from the coastal region of NSW and Victoria (AM, NHM, UC, MH, AMNH)
	Murray River (79)	Recent specimens from Roonka site, and several individuals from Murray basin River basin (SAM, NHM, UC)
	South Australia (138)	Recent Australians living near Adelaide (SAM, NHM, UC, AMNH, NMNH, MH)
	Tasmania (19)	Recent Tasmanians (AMNH, NHM, UC, MH, FM)
	Western Australia (80)	Recent Australians from Western Australia (NHM, UC, MH, AMNH)
4. North America	Subarctic (186)	From Yukon River basin, Bonasila, near Fort McPherson, Mackenzie River Delta (AMNH, NMNH, NHM)
	Northwest Coast (39)	Recent inhabitants of Northwest Coast, Kodiak Island, Tlingit, and from Vancouver Islands (NMNH, AMNH, NHM, UC, MH)
	California (118)	Sacramento, Angel Island, San Nicolas, Angeles Bay, Santa Barbara, Santa Rosa, Santa Cruz (NMNH, MH)
	Plateau/Great Basin (46)	Washington, Oregon, Utah, Colorado, Wyoming, and Nevada (NMNH, AMNH)
	Arizona (Southwest) (39)	Apache, etc., from Arizona (AMNH, NMNH)
	New Mexico (Southwest) (68)	Apache, Pueblo, Navaho, Zuni, etc. (NMNH, AMNH)
	Plains/North (123)	North and South Dakota, Montana, Iowa, Nebraska, Kansas (NMNH)
	Plains/South (94)	Missouri, Arkansas, Texas, Oklahoma (NMNH)
	Northeast Woodland/ West (104)	Illinois, Michigan, Wisconsin, Indiana, Ohio (NMNH)
	Northeast Woodland/ East (79)	New York, Massachusetts, Connecticut, New Jersey, Pennsylvania, Delaware, Maryland, Kentucky (NMNH)
	Southeast Woodland/ North (69)	Virginia, Tennessee, North and South Carolina (NMNH)
	Southeast Woodland/ South (80)	Louisiana, Mississippi, Alabama, Georgia, Florida (NMNH)

(*continued*)

Table 19.1. (*cont.*)

Large geographic groups	Local groups	Brief information
5. Central/South	America Mexico (131)	Sierra Madre of Durango, Tombat Xico, Jarasco, Tarasco, Yucatan, Duraugo, Pueblo Chihuahua, Tarahumara, Papago, Cora, Oroyo del Santa Rosa, Nixtalpa (AMNH, NMNH, NHM)
	Carib (46)	Recent Native Caribbeans from Jamaica, Cuba, Venezuela, Guyana, Guiana (NHM, NMNH, AMNH)
	Intermediate (60)	Recent Native Americans from Costa Rica, Panama, Nicaragua, Ecuador, Colombia (NMNH, AMNH, NHM)
	Peru (249)	Cerro del Oro, Cajamarquilla, San Damian, Chilca, Coyugo, Cinco Cerros, Huacho, Casa Grande, Macato, Huaras Lupo, Masca (NHM, NMNH)
	South Andes (37)	Recent Native people from Bolivia, Chile, Argentina (NMH, NMNH, AMNH)
	Fuego/Patagonia (48)	Recent Fuegians from Tierra del Fuego and Patagonians (NHM, UC, MH, NMNH, AMNH)
6. South Asia (India)	Nepal (38)	Native of Nepal (NHM)
	Assam/Sikkim (54)	Assam and Sikkim districts (NHM)
	Northeast (164)	Recent inhabitants from West Bengal Bihar and Orissa (NHM, AMNH)
	Northwest (100)	From Delhi and Punjab district (NHM, AMNH)
	Central (23)	Maharashtra, Nagpur, and Bombay (NHM, AMNH)
	Madras (112)	Recent Inhabitants of Madras, Dravidians (NHM)
	South (36)	Recent Inhabitants of Salem, Mysore, and Malabar Coast (NHM, US, AMNH)
	Veddah (27)	Veddah from Ceylon Island, Sri Lanka (NHM, UC)
7. West Asia	Afghanistan (34)	Recent Afghans from Kabul, including several individuals from Peshawar, Pakistan (NHM)
	Iran/Iraq (45)	Dailamanistan, North Iran, Islamic Peroid (UT) Recent Iraqis from Baghdad, Karbala, An Najaf (FM)
	Israel (101)	Recent inhabitants of Israel (NHM, AMNH)
	Syria/Palestine (41)	Bedouin people (AMNH, FM)
	Turkey (56)	Adalia, Aintab, Kurd, Armenian, and Mohammedan mainly from Constantinople (NHM, AMNH)
	Cyprus (32)	Roman and recent periods, Saloi (NHM, AMNH)

Table 19.1. (*cont.*)

Large geographic groups	Local groups	Brief information
8. Europe	Russia (46)	Recent Russians (NHM, AMNH)
	Czecho/Poland (53)	Moravia and Bohemia (Czecho), Silesia (Poland) (NHM, SAM, AMNH)
	Hungary (77)	Recent Hungarians from Buda-Pesth, Pressburg, Csakovar, Nagy-Sap, Demko-Hegy (NHM, AMNH)
	Romania (29)	Recent Romanians from Transylvania, Ploesci, Wallachia, Bucharest (NHM)
	Yugoslavia (27)	Herzegovina, Dalmatia, Serbia, Montenegro regions, including a few specimens from Bulgaria (NHM, AMNH)
	Greece (40)	From Tripolitza, Morea, Arta, Epirus, Athens (NHM)
	Sweden/Norway (92)	Stockholm, Oslo, Bergen, etc. (NHM, UC)
	Holland (31)	Recent Dutch from Groningen, Friesland, Amsterdam, including several individuals from Denmark and Belgium (NHM)
	Germany (50)	Recent Germans from Berlin, Mainz, Holstein (NHM, UC, NMNH)
	Austria/Swiss (67)	Vienna, Tyrol, Modling, Gloggnitz, Malta, Carinthia, and recent Swiss (AMNH, NMNH)
	Italy (143)	Recent Italians from Napoli, Firenze, Venezia, Milano, and other cities (NHM)
	France (74)	Gallo-Roman, Merovingian, and recent French; recent individuals are mainly soldiers in the army of Napoleon, including several specimens from Spain and Portugal (NHM)
	United Kingdom	Ensay (late medieval to postmedieval period, Scotland) (97) Repton (St. Wystans, Derbyshire, Northeast England) (36) Poundbury (Late Roman period, Southwest England) (114) Spitalfields (Mid-Victorian, pre-17th century, eastern regions of London) (264) (NHM, UC)
9. North Africa	Pre Dynasty (150)	Badari and Naqada, Egypt (UC)
	Early Dynasty (38)	Lisht, near Matanieh, 12th Dynasty, Egypt (NMNH)
	Middle Dynasty (115)	Cairo, Omdurman, 20th–25th Dynasty, and Gizeh, 26th–30th Dynasty, Egypt (UC, NMNH)
	Recent Egypt (36)	Kharga Oasis, Ain El Turba, El Baguat, Luxor (NMNH)
	Nubia/Dynasty (210)	Kerma, Dinka near Omdurman, 12th–13th Dynasty (UC)

(*continued*)

Table 19.1. (*cont.*)

Large geographic groups	Local groups	Brief information
	Nubia/Recent (48)	Hesa, Biga, Sesebi, after Christian date (NHM)
10. Sub-Saharan Africa	West Africa (85)	Recent West Africans from Gambia, Guinea, Ivory Coast, Liberia, Senegal, and Sierra Leone (NHM, UC, AMNH)
	Ghana/Ashanti (80)	Abuakwa, Dagomba, and Ononguna (NHM, UC, AMNH)
	Nigeria/Ibo (153)	Recent Ibo tribe from Southern Nigeria (NHM, UC)
	Cameroon/Congo (70)	Recent samples from Edia, Ibea, Mandingo, Abuakwa, Duala, Boki, Anyang, Kumabembe, Mabea (Cameroon) Recent populations from Fernand Vaz, Loango, Mobanyki, Selte Cama, Bahuana, Luano (NHM, AMNH)
	Gabon (101)	Ogove River, Fernand Vaz River basin (NHM)
	Somalia (87)	Erigavo District and Darod Kuhar, Somalia including a few specimens from recent Ethiopians (NHM, AMNH)
	Kenya (160)	Recent inhabitants of Kikuyu, Nairobi Teita Hills (UC, AMNH)
	Tanzania (151)	Recent Haya tribe from Lake Victoria Pare, Gonja, Angoni (NHM, UC, AMNH)
	Uganda (19)	Recent Teso tribe, Ankokle, Wakmia, Chif Ruakirara, including several individuals from Rwanda (Mtussi, Mhutu) (NHM, AMNH)
	South Africa (27)	Recent inhabitants from Zambia Zimbabwe, Malawi, Mozambique, Lesotho (NHM, UC, AMNH)
	Zulu (100)	Recent Zulu from Pietremanitzburg Mantatee, Tulu, Tambuki, Natal, South Africa (NHM, UC, AMNH, NMNH)
	Khoi-San (49)	Recent Bushmen and Hottentots from South Africa (NHM, UC, AMNH)

Notes:
UT, University of Tokyo, Tokyo, Japan
KU, Kyoto University, Kyoto, Japan
NHM, Natural History Museum, London, U.K.
UC, University of Cambridge, Cambridge, U.K.
MH, Musee de l'Homme, Paris, France
AM, Australian Museum, Sydney, Australia
US, University of Sydney, Sydney, Australia
SAM, South Australian Museum, Adelaide, Australia
BM, Bishop Museum, Honolulu, Hawaii, U.S.A.
NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.
AMNH, American Museum of Natural History, New York, New York, U.S.A.
FM, Field Museum, Chicago, Illinois, U.S.A.

Table 19.2. *Standards for the fifteen nonmetric dental traits*

Trait observed	Abbreviation	Criteria
1. Shoveling (UIl)	SH	The depth of lingual fossa deeper than 0.5 mm is scored as present. This classification corresponds to the categories of semi, moderate, and strong shovel employed by Hanihara et al. (1970) and grade 3–7 of the Arizona State University Dental Anthropology System (ASUDAS system) (Turner et al. 1991; Scott and Turner 1997).
2. Double shoveling (UIl)	DSH	Following the ASU system, the grade 3–6 is scored as present.
3. Shoveling (UI2)	SH	The teeth classified as the ASU system's grade 3–7 are scored as present.
4, 5. Premolar accessory cusp (UP1, UP2)	PAC	This trait is recorded following the ASU system.
6. Carabelli's cusp (UMl)	CC	Based on Dahlberg's (1963) criteria, presence (Dahlberg's d–g) is distinguished from absence (Dahlberg's a–c). The grade a–c is equivalent to 0–2 of the ASU system.
7. Hypocone (UM2)	HYC	Presence corresponds to 4- and 4+ of Plaque P9, Dahlberg (1949) and grade 3–5 of the ASU system.
8. Central ridge (LPl)	CR	Deutero-proto relationship. The scoring procedure followed is one by Higa et al. (2003).
9, 10. Sixth and seventh cusp (LM1)	C6, C7	The counting method of the two traits is the same as that of the ASU system. The cusp is scored as present regardless of the size.
11. Deflecting wrinkle (LMl)	DW	Following Weidenreich (1937), if the medial ridge of metaconid deflected distally, the trait is scored as present. Presence corresponds to grade 2–3 of the ASU system.
12. Protostylid (LMl)	PRS	The ASU system's 2–7 were scored as present.
13. Distal trigonid crest (LMl)	DTC	Following the original description by Weidenreich (1937), the crest connecting the tip of the metaconid with the distal accessory ridge of the protoconid without interruption is scored as present. This method is the same as that of the ASU system.
14. Hypoconulid (LM2)	HYCD	The counting method is the same as that of the ASU system.
15. Sixth cusp (LM2)	C6	Follows the ASU system.

2008, 2010a, b; Konigsberg 2006; Leigh et al. 2004; Nakashima et al. 2010; Pilbrow 2006).

It is well known that nonmetric variants can be regarded as threshold characters (Hauser and Stefano 1989; Konigsberg 1990; Konigsberg et al. 1993). This model assumes that the trait liability is normally distributed and can be broken by the imposition of a threshold into presence/absence states. Assuming an underlying multivariate normal distribution of liabilities, Konigsberg (1990; Konigsberg et al. 1993) estimated thresholds and variance-covariance matrices using probit analysis and tetrachoric correlation, respectively. On the basis of these studies, application of R-matrix method was extended to nonmetric dental data using tetrachoric correlation and standard deviation units derived from threshold values for each trait. Within-group variation is estimated using bootstrap resampling of the original data in each group with 1,000 replications. More background on the R-matrix method, within-group nonmetric variation, and bootstrapping is presented elsewhere (Hanihara 2010a, b; Nakashima et al. 2010).

To conduct R-matrix analysis, an estimate of average heritabilities for phenotypic traits is required. In this study, the average heritability of $h^2 = 0.50$ was used for metric and nonmetric data. The validity of the heritability estimates is detailed elsewhere (Hanihara 2008, 2010a, b; Hanihara and Ishida 2005).

The geographic assignment tests were analyzed using linear regression analysis for dental gradients and the relationships between degree of diversity and biological/geographic distances from sub-Saharan Africa. Moreover, an isolation-by-distance model (Relethford, 2004a) was applied to examine the correlation between geographic and phenotypic distance and to confirm the relevance of the estimated dispersal route. This is all based on the fact that geographic distance limits migration between populations, resulting in a regular decrease of genetic (and phenotypic) similarity with increasing geographic distance (Eller 1999; Relethford 2004a, b, 2009, 2010; Liu et al., 2006; Serre and Pääbo 2007; Novembre et al. 2008). This model, the least-square nonlinear regression analysis (exponential approximation), is expressed in terms of the elements of R-matrix and related parameters as follows:

$$rij = (Fst - rmin)\, e^{-bd} + rmin.$$

Under isolation by distance, the expected correlation between population i and j is of the form ke^{-bd}, where d is the geographic distance between the two populations and b is the rate of distance decay.

For each pair of regional samples, geographic distance was measured in kilometers based on great circle distances (Relethford 2004; Manica et al.

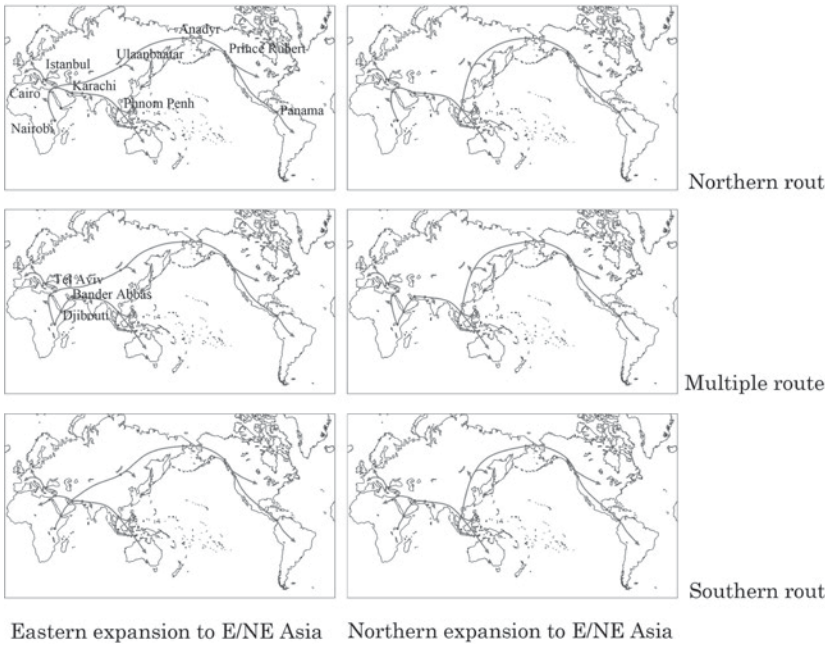

Figure 19.1. Map showing waypoints and possible colonization routes through them.

2005; Ramachandran et al. 2005). Pairwise geographic distances were calculated using twelve waypoints, as shown in Figure 19.1, to make estimates of between-regional population distances more reflective of human migrations (Ramachandran et al. 2005; Cramon-Taubadel and Lycett 2008). The distance between two regions is the sum of the great circle distance between the regional center of each geographic region and the waypoint in the path connecting them, plus the great circle distances between waypoints if two or more waypoints exist (Ramachandran et al. 2005). That is, the geographic center of local samples within each regional cluster is taken as the geographic coordinate of that cluster; the great circle distances are then computed between these ten geographic points, adjusting for waypoints. The point of origin for modern humans is tentatively set in Nairobi, Kenya, a likely region for the origin of anatomically modern humans (Harpending et al. 1993; Yuehai et al. 2001; Prugnolle et al. 2005; Ramachandran et al. 2005; Liu et al. 2006; Mellars 2006).

Several dispersal routes are assumed here, including the combination of three routes for out of Africa migration, that is, northern, southern, and

multiple routes, and two possible colonization routes for East/Northeast Asia, that is, eastern expansion from western or central Asia via the Siberian route and the northern expansion from Southeast Asia. As shown in Figure 19.1, the first (northern) route is along the Nile River, across the Sinai peninsula and Levant, into western Asia, Europe, the northern part of eastern Eurasia and the New World via the Bering Strait, and Southeast Asia along the Indian Ocean coastline and Australasia via the Wallace Strait (Jones et al. 1992; Kingdon 1993; Lewin 1993). The second route, known as the multiple exodus hypothesis, also includes a northern route via the Levant to Europe, northeastern Asia, and finally the New World; yet it also covers an earlier southern route from eastern Africa to Southeast Asia and Australia along the Indian subcontinent across the Bab-el-Mandeb Strait into southern Arabia and the South Asian coast (Lahr and Foley 1994; Lahr 1996; Quintana-Murci et al. 1999; Stringer 2000; Underhill et al. 2001; Luis et al. 2004; Forster and Matsumura 2005; Thangaraj et al. 2005; Macaulay et al. 2005). The third is a single southern route out of Africa via the Bab-el-Mandeb Strait, to Southeast Asia and Australia, from the Arabian Gulf to the Levant and Europe and Northern Africa, and to eastern/northeastern Asia via central Asia through southern Siberia (north of the Himalayas), and finally the New World via the Bering Strait (Chandrasekar 2007; Uinuk-Ool et al. 2003;Wells 2002). These three routes hypothesize that the southern and northern populations in eastern Asia arrived essentially from different areas (Brace et al. 2001; Deng 2004; Forster et al. 2001; Karafet 2001; Xue et al. 2006, 2008). Beyond the eastward migration from western/central Asia via the southern Siberian route after the Africa exodus, the present study assumes the northward extension of Southeast Asians for the peopling of East/Northeast Asia and finally the New World as shown on the right side of Figure 19.1 (Chu 1998; Jin and Su 2000; Oppenheimer 2003; Shi et al. 2005; Su et al. 1999; HUGO Pan-Asian SNP Consortium 2009; Turner 1987, 1990, 1992).

19.3 Results

Applying the R-matrix approach, the minimum and estimated Fst values based on average heritability of 1.0 and 0.5 with their standard margin of errors, respectively, for metric and nonmetric data sets are listed in Table 19.3. The Fst values, representing interregional variation, fall within a range between 0.0528 and 0.2570. The Fst is somewhat greater for nonmetric than metric data. As a whole, the majority of diversity of major populations exists within regions,

Table 19.3. *Minimum and estimated Fst values for metric and nonmetric dental data*

	Minimum Fst	S.E.	Estimated Fst	S.E.
Metric	0.0528	0.0015	0.1002	0.0019
Nonmetric	0.1474	0.0349	0.2570	0.0375

Table 19.4. *Observed, expected, and residual variances based on metric dental data*

Sample names	Observed variance	Expected variance	Residual variance	S.E.
North America	0.9433	1.0239	–0.0806	0.0200
Central/South America	0.9791	1.0839	–0.1048	0.1262
East/Northeast Asia	0.9394	1.2300	–0.2906	0.0268
Southeast Asia	1.0829	1.2621	–0.1792	0.0151
Australia	1.0012	0.2567	0.7445	0.0838
South Asia	0.9654	1.0779	–0.1125	0.0208
West Asia	1.0354	0.9966	0.0389	0.0256
Europe	0.9346	0.7707	0.1639	0.0176
North Africa	1.0259	1.2129	–0.1870	0.0241
Sub-Saharan Africa	1.1492	1.1417	0.0074	0.0206

compatible with those measured by genetic and craniometric data (Relethford 1994, 2002).

Table 19.4 gives intraregional variations and related values based on odontometric data. The sub-Saharan African sample shows the largest within-group variation, followed by Southeast Asian and West Asian samples. On the other hand, European, East/Northeast Asian, and New World samples show relatively low intraregional variation. Estimates of intraregional variations based on the nonmetric dental data are shown in Table 19.5. The results parallel those obtained by metric data. The sub-Saharan sample again shows the largest within-group variation, followed by that of Southeast Asia.

Following the largest within-group diversity in sub-Saharan Africa, the relationship between phenetic and geographic distance is examined by applying simple regression analysis. Figure 19.2 shows the relationship between the degree of intraregional variation and geographic distance from Nairobi, Kenya, under the northern route hypothesis for out of Africa and northern expansion of Southeast Asians versus eastern migration of central/western

Table 19.5. *Observed, expected, and residual variance based on nonmetric dental data*

Sample names	Observed variance	Expected variance	Residual variance	S.E.
North America	0.001101	0.000851	0.000250	0.000001
Central/South America	0.001064	0.001063	0.000001	0.000001
East/Northeast Asia	0.001253	0.001216	0.000037	0.000001
Southeast Asia	0.001300	0.001520	–0.000220	0.000000
Australia	0.001232	0.000936	0.000295	0.000001
South Asia	0.001098	0.001462	–0.000364	0.000001
West Asia	0.001188	0.001107	0.000082	0.000001
Europe	0.001081	0.001178	–0.000098	0.000001
North Africa	0.001070	0.001073	–0.000002	0.000001
Sub-Saharan Africa	0.001392	0.001373	0.000019	0.000001

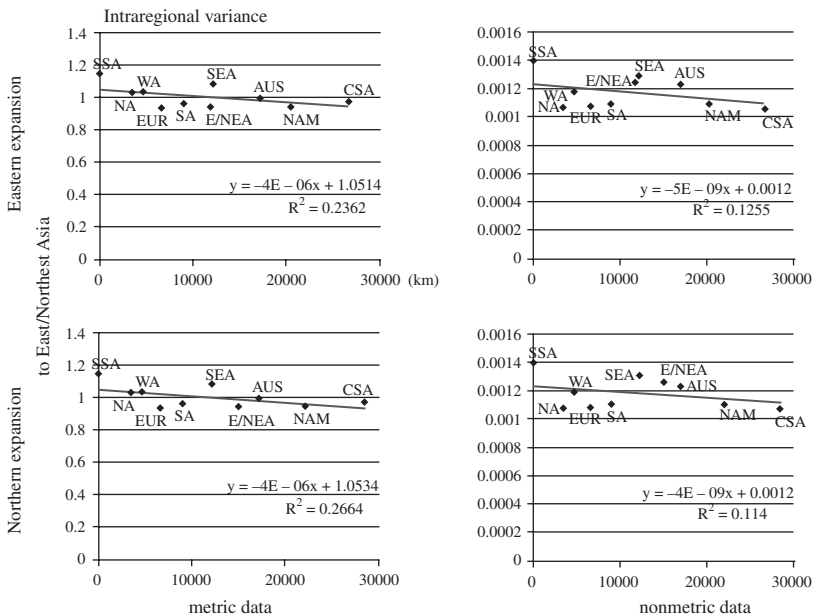

Figure 19.2. Relationships between intraregional variation and distance from sub-Saharan Africa based on northern route hypothesis for Africa exodus. Abbreviations: SSA, Sub-Saharan Africa; NA, North Africa; WA, West Asia; EUR, Europe; SA, South Asia; SEA, Southeast Asia; E/NEA, East and Northeast Asia; AUS, Australia; NAM, North America; CSA, Central and South America. The same abbreviations are used in Figures 19.3 through 19.7.

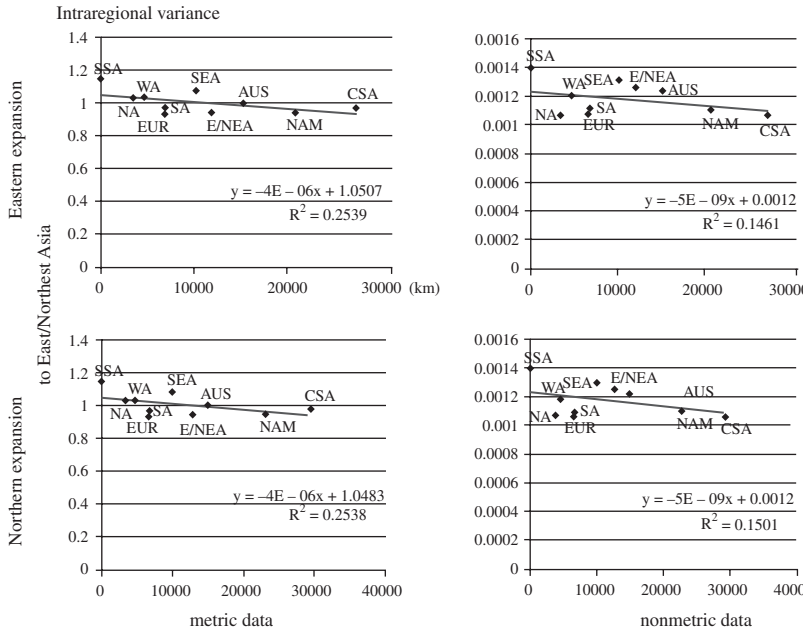

Figure 19.3. Relationships between intraregional variation and distance from sub-Saharan Africa based on multiple route hypothesis for Africa exodus.

Asians for the peopling of East/Northeast Asia. In both cases the correlations are very weak and nonsignificant. The regression analysis was then performed under the hypothesis of multiple routes (Figure 19.3). The R^2 values are similar to those in Figure 19.2, suggesting very weak correlation between intraregional variations and geographic distances from sub-Saharan Africa in the ten major populations. Figure 19.4 shows that the single southern route hypothesis yields inverse linear relationships, with the highest correlation between within-group dental variance and geographic distance. In metric data, the northern expansion model for the peopling of East/Northeast Asia shows higher correlation than the eastern model. The reverse is true, however, for nonmetric data.

The next analysis focuses on the relationship between geographic distance and R-matrix based phenotypic distance from sub-Saharan Africa to major geographic regions. Figures 19.5–19.7 show such relationships of geographic-phenotypic distances in the case of northern, multiple, and southern routes for out of Africa migration. Under both the northern and multiple route hypotheses, correlations between geographic and phenotypic distances are weak

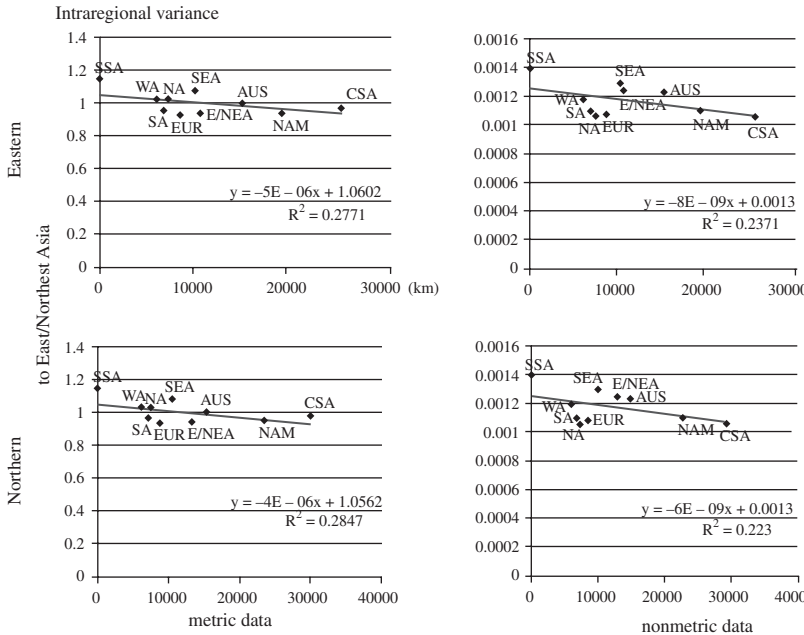

Figure 19.4. Relationships between intraregional variation and distance from sub-Saharan Africa based on southern route hypothesis for Africa exodus.

for metric dental traits. The linear regression analysis based on the southern route hypothesis gives the highest R^2 values for both metric and nonmetric data (Figure 19.7). Moreover, the eastern expansion model for peopling East/Northeast Asia shows a higher correlation than the northern expansion model for metric data.

The two kinds of regression analyses suggest that isolation by distance should have an effect on average patterns of dental morphological variation, at least under the southern route hypothesis for out of Africa. Given such background, the analysis of the relationships between patterns of phenotypic variation and geographic distance is extended to the isolation-by-distance model of Relethford (2002). On the basis of the findings in Figures 19.2–19.7, this method is applied to the southern route for the African exodus. Figure 19.8 shows the relationship between r_{ij} and geographic distance between every pair of samples for metric and nonmetric data. For each data set, the isolation-by-distance model is fitted using nonlinear regression or exponential approximation. The two data sets roughly show the expected decline in biological similarity with geographic distances. This finding suggests the

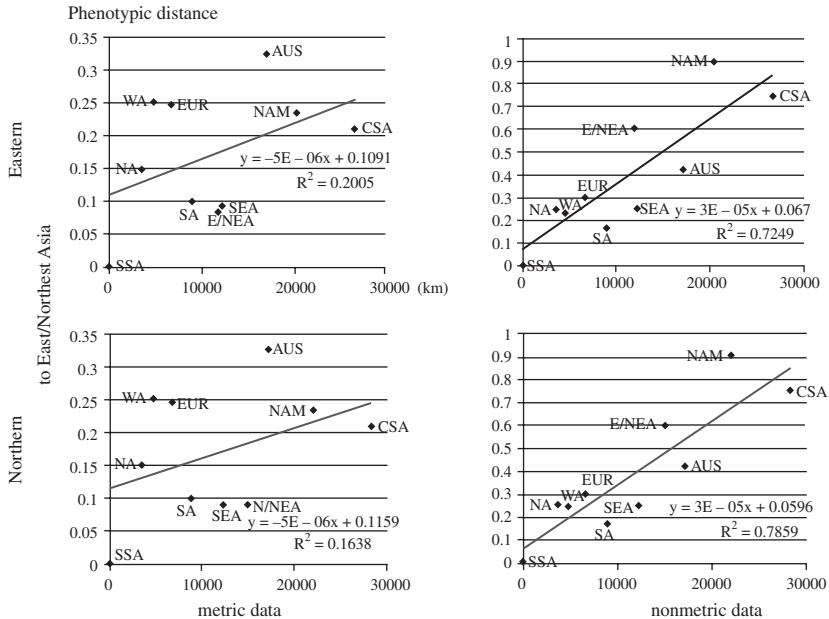

Figure 19.5. The relationship between phenotypic and geographic distance from sub-Sahara Africa to major geographic regions under the northern route hypothesis for out of Africa model.

importance of a southern dispersal route for emigration out of Africa and subsequent expansion along the shorelines of Arabia toward Southeast Asia and eventually Australia, on the one hand, and into Europe and North Africa through the Levant region, on the other.

Finally, a possible pattern of interpopulation relationships on a global scale is examined using a distance matrix transformed from the R matrix on the basis of metric data and a network Splits Tree presentation. The splits graph in Figure 19.9 reveals that the sub-Saharan African sample is not the most highly differentiated group. In terms of overall metric dental differences, the two world extremes are Australia and the New World. Moreover, the Southeast Asian and East/Northeast Asian samples are closely related.

Similar results were obtained by applying the same method to nonmetric data (Figure 19.10). In this case, the distance between Southeast Asia and East/Northeast Asia is larger than that measured by metric traits. This result may indicate a more complex population history of East/Northeast Asia than suggested by the simple northern expansion hypothesis.

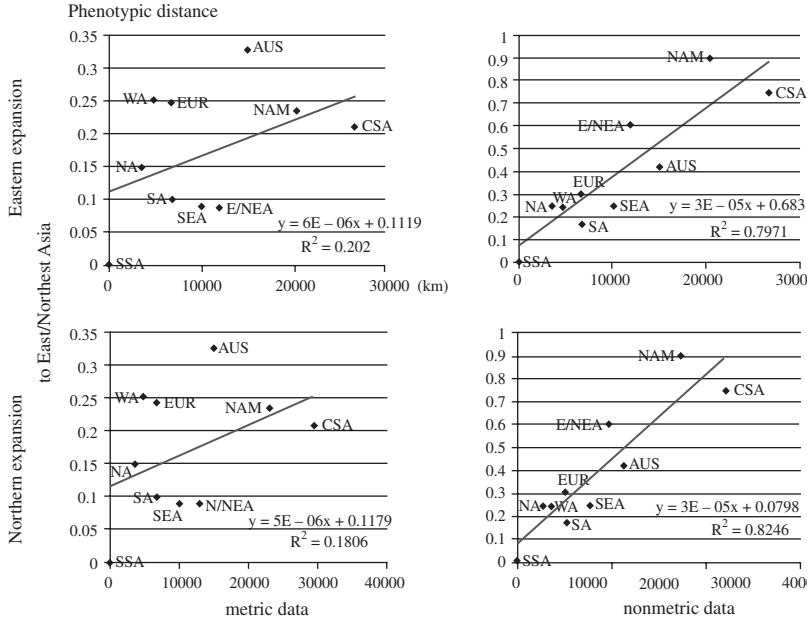

Figure 19.6. The relationship between phenotypic and geographic distance from sub-Sahara Africa to major geographic regions under the multiple route hypothesis for out of Africa model.

19.4 Discussion

Relatively low interregional diversity estimated by Fst among world groups and the largest intraregional variation in sub-Saharan Africa suggest that the underlying patterns of population structure assessed by dental features fit, as a whole, a neutral model. Such findings may allow us to regard the present patterns of dental diversity as a predictor for inferring possible population history, including colonization routes from Africa to major geographic regions – with special reference to the peopling of East/Northeast Asia.

The recent African origin hypothesis for anatomically modern humans implies a rapid expansion with serial bottlenecks, leading to a decrease of genetic and phenotypic diversity with increasing distance from Africa along possible colonization routes (Li et al. 2008; Liu et al. 2006; Manica et al. 2005, 2007; Prugnolle et al. 2005; Relethford 2004a; Serre and Pääbo 2004). The orthodox interpretation of dispersals from Africa favors the route along the Nile and Sinai peninsula leading into the Levant (Cavalli-Sforza et al. 1994; Jones et al. 1992; Lewin 1993; Luis et al. 2004; Manni et al. 2002; Salas et al.

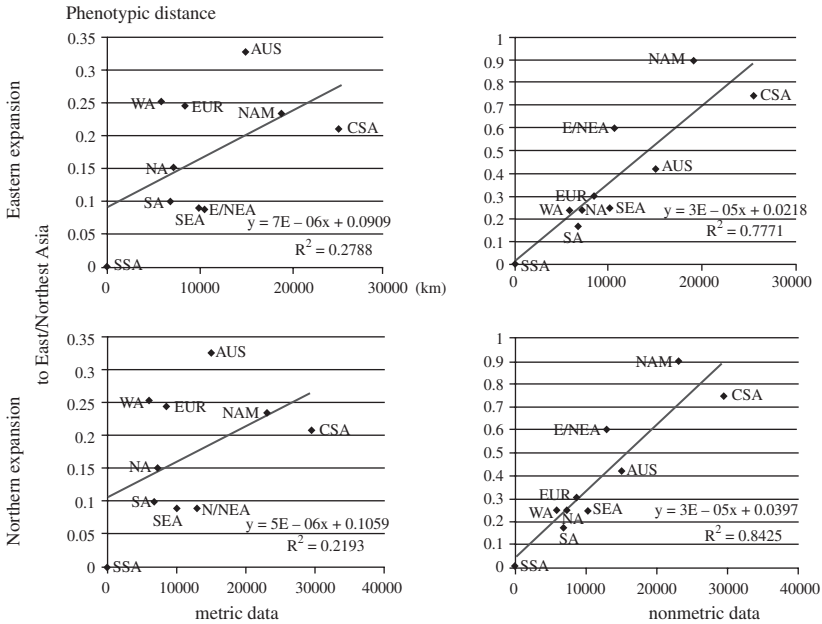

Figure 19.7. The relationship between phenotypic and geographic distance from sub-Sahara Africa to major geographic regions under the southern route hypothesis for out of Africa model.

2002). Recent mtDNA analysis suggests the route across the Bab-el-Mandeb Strait and Indian Ocean coastline (Forster and Matsumura 2005; Hudjashov et al. 2007; Oppenheimer 2003; Stringer 2000). Oppenheimer (2003) regarded the southern region of the Zagros Mountains, part of the Fertile Crescent, as a core homeland for early modern Europeans and North Africans and emphasizes that the route of entry into Europe and North Africa was most likely via the Levant. The present findings indicate that modern dental variation patterns fit a model of iterative founder effects along the colonization route taken from Africa to Eurasia across the Horn of Africa and subsequent southwestern Asian regions.

Under the southern route hypothesis for out of Africa, increasing dissimilarities between populations with geographic distance are confirmed by the isolation by distance model in both metric and nonmetric data (Figure 19.7). Such results support the southern route hypothesis for out of Africa. However, correlations between geographic and pairwise biological distances are moderate, and some populations do not strictly fit the model. Deviations from the fitted line may be explicable not only by admixture, genetic drift, isolation,

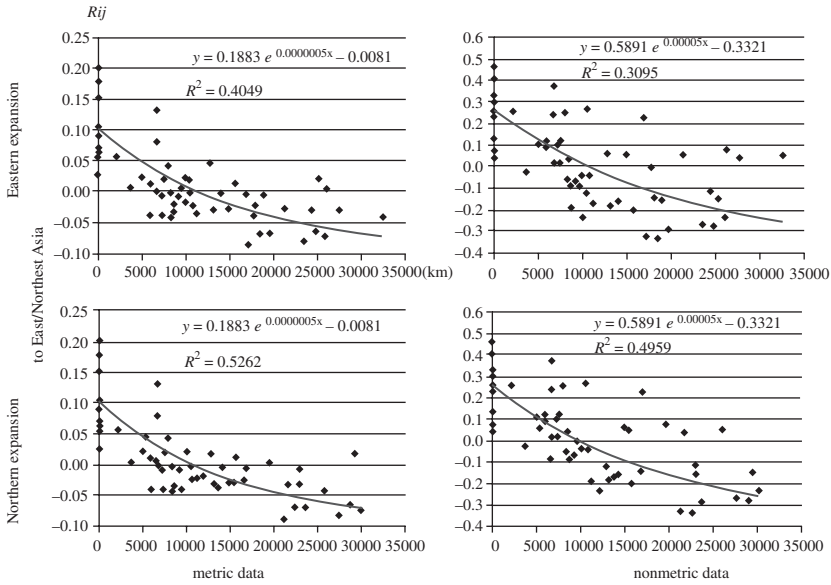

Figure 19.8. The relationship between r_{ij} and geographic distance between every pair of samples in metric and nonmetric dental samples on the basis of the southern route hypothesis. For each data set, the isolation-by-distance model is fitted by using nonlinear regression analysis (exponential approximation).

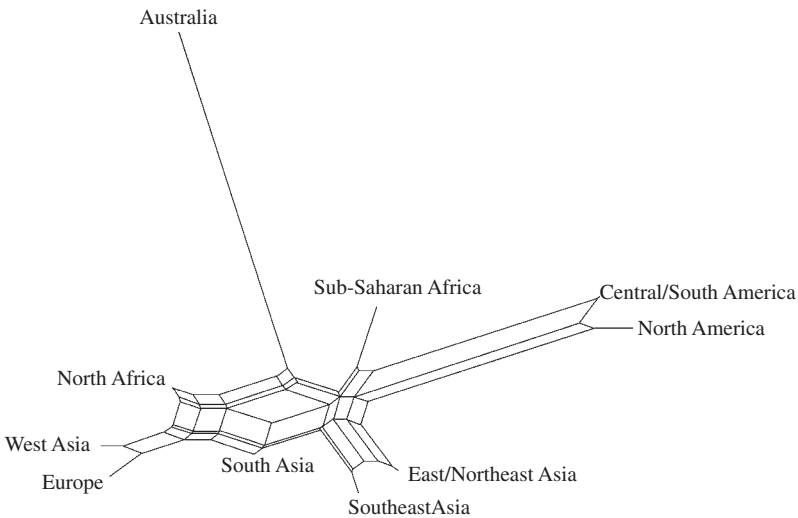

Figure 19.9. Interpopulation relationships on a global scale using distance matrix transformed from the R matrix and network Splits Tree presentation based on the metric dental data.

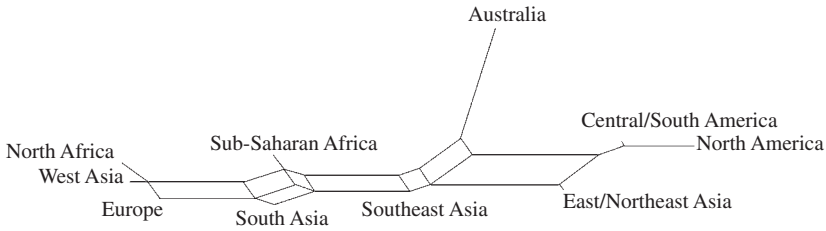

Figure 19.10. Interpopulation relationships on a global scale using distance matrix transformed from the R-matrix and network Splits Tree presentation based on the nonmetric dental data.

and other factors related to genetic control, but by population-specific natural selection related to environmental influence and subsistence patterns (Harvati and Weaver 2006; Hubbe et al. 2009; Relethford 2004b, 2009, 2010). The interpretation of genes and selection in shaping phenotypic traits will be discussed later.

The extremities and deep branching pattern of the Australian cluster, together with a relatively larger variance than expected, may shed light on the route and timing for the exodus from Africa. The distinctiveness of Australian dental features may be attributed to (1) the retention of genetic and morphological characteristics linked to early modern humans from sub-Saharan Africa (Hanihara 1996; Hudjashov et al. 2007; Howells 1989; Lahr 1996); (2) an earlier expansion of the founding African population to Australia through a "coastal expressway" and isolation after the initial arrival there (Chandrasekar et al. 2007; Forster and Matsumura 2005; Forster et al. 1998; Hudjashov et al. 2007; Lahr 1996; Macaulay et al. 2005; Quintana-Murci et al. 1999; Rasmussen et al. 2011; Stringer 2000; Wells 2002); or (3) a time function accumulating within-group variation (Relethford and Harpending 1994).

Another important issue is the expansion and colonization process in eastern Asia. Intraregional variation of Southeast Asians and, to a lesser extent, East/Northeast Asians (Tables 19.4 and 19.5) is relatively large. Such results may reflect a complex population history in these regions. It is generally held that genetic and morphological features of Southeast Asians have some relation to episodes of gene flow from the west during the late Pleistocene; this input would have occurred after initial colonization of the region by Australians, ca. 50,000–70,000 year B.P. (Lahr 1996; Rasmussen et al. 2011; Soares et al. 2008; Underhill et al. 2001; Wells 2002), as well as the spread of Austroasiatic-speaking agriculturalists from southern China in the middle to late Holocene (Capelli et al. 2001; Endicott et al. 2003; Hill et al. 2006, 2007; Lahr 1996; Matsumura and Hudson 2005; Turner 1990). These arguments

suggest that a relatively high level of average divergence in recent Southeast Asians can be attributed to complex patterns of ancient migration, together with demographic history, such as a long-term large effective population size related to agricultural dispersals (Ding et al. 2000; Peng et al. 2010).

One of the most controversial issues in eastern Asia may be the establishment of the origins and migration routes of East/Northeast Asians. Many genetic and morphological studies regard Southeast Asia as the major source for the peopling of East/Northeast Asia (Ballinger et al. 1992; HUGO Pan-Asina SNP Consortium 2009; Su et al. 1999; Shi et al. 2005, 2008; Turner 1987, 1990). However, recent global analyses based on extensive genetic and morphological data detect central Asian and/or western Eurasian components in East/Northeast Asian physical characteristics (Di and Sanchez-Mazas 2011; Karafet et al. 2001; Nakashima et al. 2010; Uinuk-ool et al. 2002; Zhong et al. 2011). The results obtained in this study are consistent with a southern-origin hypothesis for East/Northeast Asians. However, relationships between geographic distance and biological distance/variation do not exclude the possibility of migration from western Eurasia into East/Northeast Asia via the northern Siberian route. The network based on nonmetric dental traits (Figure 19.10) suggests a possible phenotypic separation of East/Northeast Asians from Southeast Asians. Such findings indicate that although the northern expansion from Southeast Asia played a major role in human settlement in East/Northeast Asia, there are additional contributions.

When morphological characteristics are discussed, one should pay attention to the extent to which environmental factors shaped phenotypic features, especially in the case of northeastern Asians (Harvati and Weaver 2006; Hubbe et al. 2009; Noback et al. 2011; Roseman 2004; Roseman and Weaver 2004). Although there is little doubt that morphological variation is more or less affected by natural selection (e.g., Beals et al. 1984; Carey and Steegmann 1981; Guglielmino-Matessi et al. 1979; Harvati and Weaver 2006; Roseman 2004), adaptive responses to different selective forces over time cannot be directly tested. However, as emphasized by Relethford (2004b), different environmental influences on phenotypic variation do not erase or obscure the influences under genetic control (Hanihara 2010b; Sparks and Jantz 2002; Weaver et al. 2008). Present results suggest that the same may be true in the case of metric and nonmetric dental features.

Finally, possible genetic and phenotypic contributions of archaic humans (e.g., Neanderthals and Denisovans) to recent human populations should be considered in future attempts to estimate modern human variation and diversity (Abi-Rached et al. 2011; Green et al. 2010; Reich et al. 2010; Soficaru et al. 2007; Yotova et al. 2011).

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20 *New approaches to the use of dental morphology in forensic contexts*

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20.1 Introduction

Dental morphology, as the term is generally used in anthropology, considers observations of minor structures of the tooth crown and root, including grooves, ridges, and cusps (Scott and Turner 1997). Most researchers utilize these data as a tool for studying population variation. Dental anthropologists use many characteristics of the tooth and relatively sophisticated statistics to describe how much variation exists within and between populations. The intent is to understand how populations may be related, especially ancestor-descendant relationships. As data, observations of dental characteristics are good for this purpose because they are at least in part heritable and do not change (except through wear or caries) after a tooth is developed (Hillson 1996; Scott and Turner 1997). Additionally, dental morphological characteristics are evolutionarily conservative and generally neutral (Hillson 1996; Scott and Turner 1997; but see Kimura et al. 2009 and Mizoguchi 1993, 1985, this volume), and directly comparable across space and time, including contemporary specimens. These same characteristics make dental traits good potential tools for use in forensic contexts.

Teeth are used in forensic cases to address questions about unknown persons. Because teeth develop in a canalized manner and show a high correlation between developmental age and chronological age, they can be used to estimate the age of a juvenile (Al Qahtani et al. 2010; Moorrees et al. 1963). Tooth wear is also used as an indicator of age in adults (Prince et al. 2008; Scott 1979). Tooth size varies between males and females within a population (especially for the canine), but the differences are small (2–6 percent). For that reason, researchers have had mixed success using measurements

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as an indicator of sex (Ditch and Rose 1972; Garn et al. 1964, 1977, 1979; Kieser 1990; Rösing et al. 1995). Forensic odontologists use patterns of tooth shape, restorations, and other indicators in dental records to make positive identifications (Furuhata and Yamamoto 1967; Herschaft et al. 2007).

An additional and underutilized forensic application of dental data is in the estimation of race in unidentified human remains. Here "race" refers to a social group that a person is ascribed to by others. Ascription to this group is based on a number of factors, both cultural (e.g., accent and style of dress) and biological (e.g., skin color and facial features), and is time and place specific. Biological factors used in race ascription but absent in skeletal remains, such as skin color, are correlated with other biological features, including dental morphological traits, that are not commonly used in ascription but that remain post mortem. These traits are correlated with one another and socially recognized groups result from our species' history of migration and serial founder effects (Hanihara 2008; Ramachandran et al. 2005). In the United States, these evolutionary patterns have been partially maintained as a result of positive assortative mating and institutional racism.

Forensic anthropologists are often called upon to estimate the race to which a set of unknown remains would have been ascribed to during life. They need to know the answers to two specific questions: (1) to which socially ascribed race would this person belong and (2) how probable is that assessment? Dental morphological characteristics provide important clues for answering these questions. Biological characteristics, such as genetic markers, cranial variation, and dental morphology, provide indicators of genetic ancestry. Because of the demographic history of our species, many dental characteristics vary in frequency depending on the geographic area of the population from which individuals derive. A researcher interested in estimating race of an unknown individual can examine a dentition for clues about individual ancestry. However, ancestry does not equate to race, and the error of estimate between the two is unknown.

Relative to craniometric analysis, the use of dental morphology quantitatively to estimate the race of skeletal remains is rare (Schmidt 2008; but see Edgar 2005). Unfortunately, until now, much of the forensic use of dental characteristics has been nonscientific: that is, it has not been based on reproducible studies that provide results and associated error rates. The use of dental morphology in forensics has been mainly qualitative, with one or two characters included among cranial variables and overall skull shape to assess race. This kind of evaluation is a form of experiential Bayesian classification, where the observer weighs in his/her mind a variety of factors that affect the likelihood of an unknown individual's belonging to any particular race. In addition to morphological characters, the observer may consider

where the remains were found, variation in the living population of that area, prior experience with characteristics in specific groups, cultural indicators with the remains, and any number of other subjective factors. Classification then proceeds nonstatistically, based on comparisons with trait frequencies in each group for each category of information, weighted by the observer's understanding of the relative importance and reliability. However, correlation among trait frequencies and categories is not well understood and may not always be considered, resulting in reduced power and unknowable confidence in results.

The intent of this chapter is to explore statistical techniques that allow investigators to meet the criteria for scientific testimony set forth in *Daubert v. Merrell Dow Pharmaceuticals* (No. 92–102 509 US 579, 1993) regarding the use of dental morphology to estimate the ancestry of unidentified human skeletal remains. Applied strictly to scientific testimony, the *Daubert* criteria are important for researchers who want to practice good science in their forensic evaluations. These criteria concentrate on the reliability of observations and validity of methods, neither of which is 100 percent (Foster and Huber 1999). Data reliability refers to repeatability in recording observations; highly reliable observations are those with low intra- and interobserver differences. Reliability is achieved generally through standardized definitions and practice. The validity of a method is a measure of how often it produces correct conclusions; an estimate of validity can be obtained by the correct classification rate when the method is applied to a reference sample. Analyzing multiple traits results in a higher correct classification rate than analyzing a single trait; this approach helps prevent sampling bias: the estimated validity applies to future uses of a method as well. Naturally, methods with higher validity are preferred, but the error rates of different methods must be estimated and compared to choose the best one. Most importantly, a researcher following the *Daubert* guidelines will have an estimated probability of reaching the correct conclusions and can weigh the latter accordingly. In contrast, the current use of dental morphology in forensics is largely limited to qualitative assessments, such as "probable" European ancestry due to the presence of a Carabelli's cusp.

The present research is an effort to improve the validity of dental morphological analysis in forensic estimations of race. Toward this end, we utilize a wide array of characteristics beyond incisor shoveling and Carabelli's trait. We couple those observations with several statistical approaches to yield estimates of an unknown individual's ancestry and the estimated probability of correct classification. Some statistics we employ are traditional, while others have only been recently used to answer questions in forensic anthropology.

20.2 Material

Because of secular changes in populations, methods developed for medicolegal applications should be tested on contemporary or recent samples. Materials used in this study date to the current and twentieth centuries. They are dental models (casts) from living persons and represent contemporary African Americans (AfA), Asian Americans (AsA), European Americans (EuA), Hispanic Americans from the southeastern United States (HSE), Hispanic Americans from the western United States (HW), and Native Americans (NA). The AfA and EuA samples are derived from collections in several areas of the country. NA samples, however, are confined to the Southwest.

Group membership was assigned for each individual by a member of his or her community. Here, AfA refers to people thought to have a substantial portion of their ancestry traceable to individuals forcibly moved from West Africa to the United States since 1492. EuA are people with ancestry that is overwhelmingly exclusive to Europe. HSE and HW refer to those who have some part of their ancestry originating in Spanish-speaking regions, including Cuba, Mexico, Puerto Rico, Central America, or South America. Hispanics in different areas of the United States have different patterns of continental ancestry. For example, Florida Hispanics are predominantly from Cuba, Puerto Rico, and the Caribbean; their ancestry is primarily from Africa and Europe, much like that of AfA individuals. Hispanics in the Southwest, however, are chiefly from Mexico or have long family histories in the U.S. territory (Bertoni et al. 2003). Their ancestry is Native American and European, with only small contributions from Africans. For this reason, samples from South Florida and New Mexico are treated independently.

Composition of each group is expected to approximate those described by the U.S. Census (2010) with regard to ethnicity first and race second (which is related to ancestry to a degree). For example, HSE and HW are considered Hispanic (i.e., an ethnicity in the census), despite the fact that HSE are more likely to be classified as Black ([the census term] African-American); HW are more likely to be classified as White (European American) or Native American. Our approach recognizes the value of group membership to aid in forensic identification but bears in mind the role of self-identification. For example, in 2000, 42 percent of New Mexico census respondents who designated themselves as Hispanic chose "Other" for their race; however, in 2010 only 32 percent of the same group did so (U.S. Census 2010). These results illustrate the fluctuating nature of race attribution and present a cautionary note to all who attempt to study it.

How each individual was assigned is described in the sample descriptions that follow. In most cases, a subject's orthodontist, who had direct interactions

with the individual and knew his or her name, made a group assignment. Previous research has estimated the accuracy of medical practitioners' knowledge of their patients' race and ethnicity by examining the frequency with which two observers agree about an individual's assignment. Such work has shown that medical records created by practitioners much less familiar with patients than these orthodontists are in good agreement for EuA and AfA (~90 percent) and are less reliable for Hispanics (35–75 percent) (Baumeister et al. 2000; Blustein 1994; Hahn et al. 1992; Kressin et al. 2003).

20.3 Collections used

Arizona State University (n = 61 NA): the materials are from two collections, the Pima dental casts collected by Albert Dahlberg in the 1940s–1950s (n = 30) and the Keams Canyon Navajo collected by Christy Turner and Richard Scott between 1968 and 1971 at a clinic on the Hopi Reservation (n = 31) (G. Richard Scott, personal communication, 2011).

Case Western Reserve University (n = 54 EuA): these casts are part of the large Bolton-Brush Longitudinal Growth Study collection. The casts represent individuals born in Cleveland, Ohio, in the 1920s and 1930s (Behrents and Broadbent 1984).

Economides Orthodontic Collection (n = 90 HW): the casts are part of a large collection (n ~ 6,000) at the Maxwell Museum of Anthropology, University of New Mexico; some are available at http://hsc.unm.edu/programs/ocfs. An orthodontist in private practice collected the casts from 1972 to 1999 and donated them to the museum in 2005. Most patients were adolescents or young adults at the time. Graduate and undergraduate students working in the Laboratory of Human Osteology estimated that the subjects in this sample are Hispanic on the basis of patient records, which include full facial photographs and names. This study only includes individuals for whom at least two students agreed on affiliation. Overall agreement between observers that a subject was Hispanic was 84 percent (Edgar et al. 2011).

Nova Southeastern University (n = 201 HSE): orthodontic students took these casts when treatment was performed at a dental school near Ft. Lauderdale, Florida. All individuals were patients at the time (2009), and most were adolescents or young adults. The treating orthodontist determined group affiliation for each patient.

Ohio State University (n = 55 AfA): dental cast collections at OSU include several hundred donated by Renee Menegaz-Bock, who collected them while working with Albert Dahlberg. Dentitions of Gullah people, African Americans from the Outer Banks of South Carolina, were cast in the 1950s as part of

Table 20.1. *Samples used in this study*

Group	Code	n	Sample	Sample n
African American	AfA	230	Gullah	55
			Western	75
			Southern	100
Asian American	AsA	71	Western	71
European American	EA	155	Northern	54
			Southern	101
Hispanic American	HSE	379	Southeastern	201
	HW		Western	178
Native American	NA	61	Western	61
			total	896

a larger study of their ancestry and biology. This analysis includes observations of people born in the 1920s through 1940s (Menegaz-Bock 1968). Since genealogies are available, casts were selected to ensure that individuals were not related.

University of Southern California (n = 64 AfA, 68 AsA, 81 HW): orthodontic students took these casts when treatment was performed at a dental school in Los Angeles, California. All individuals were patients at the time (2010), and most were adolescents or young adults. The treating orthodontist determined group affiliation for each patient.

University of Tennessee, Memphis, Health Science Center (n = 100 AfA, 101 EuA): this collection includes 300–400 dental casts from modern European Americans and African Americans. They were taken in association with orthodontic work performed at the dental school. Most individuals were adolescents or young adults in the last two decades of the twentieth century (Edward Harris, personal communication, 2002).

Table 20.1 presents a summary of each sample by race and region.

20.4 Methods

20.4.1 Observational methods

Using the expression count method (Turner 1985), one author (HE) made 90 observations of the left and right antimeres in 896 dentitions. From these, the eighteen characteristics that best discriminate among samples were included in further analysis. All traits are common ASUDAS variants (Turner et al. 1991). See Table 20.2 for a listing of traits. Most are scored on ordinal scales, though

Table 20.2. *Dental traits observed with associated breakpoints and scoring type*

Trait	Code	Absent	Present	Scoring type
Winging	WING	3	1–2	Categorical
UI1 Labial curvature	UI1LC	0–1	2–4	Ordinal
UI1 Shoveling	UI1SS	0–1	2–7	Ordinal
UI2 Shoveling	UI2SS	0	1–6	Ordinal
UC Shovel	UCSS	0–1	2–7	Ordinal
UI1 Double shovel	UI1DS	0	1–6	Ordinal
UI2 Double shovel	UI2DS	0–1	2–7	Ordinal
UP1 Accessory cusps	UP1AC	0	1–3	Categorical
UM1 Metacone	UM1MC	0–4	5–6	Ordinal
UM1 Hypocone	UM1HC	0–4	5–6	Ordinal
UM1 Cusp 5	UM1C5	0	1–5	Ordinal
LI1 Shoveling	LI1SS	0	1–7	Ordinal
LI2 Shoveling	LI2SS	0	1–7	Ordinal
LP1 Lingual complexity	LP1LC	0–1	2–9	Mixed ordinal/categorical
LP2 Lingual complexity	LP2LC	0–1	2–9	Mixed ordinal/categorical
LM1 Groove pattern	LM1GP	0–1	2–6	Ordinal
LM2 Groove pattern	LM2GP	0	1	Categorical
LM2 Cusp number	LM2CN	x, +	y	Categorical
LM1 Protostylid	LM1PS	x, +	y	Categorical
LM2 Protostylid	LM2PS	0	1–7	Ordinal
LM1 Trigonid crest	LM1TC	1–3	4–6	Ordinal
LM2 Cusp 7	LM2C7	0	1–4	Ordinal

some are categorical in nature, or their scoring reflects a combination or categorical and ordinal character state change. The Appendix provides information on sample sizes, dichotomized trait frequencies, and score frequencies for each group by trait.

Dental morphological data are often dichotomized for statistical analysis, including calculating frequencies and assessing relationships among groups using the mean measure of divergence or pseudo-Mahalanobis distances (Konigsberg 1990). Dichotomizing observations, however, is recognized as limiting our ability to represent or understand variation (Mayhall 1999). There are traditional breakpoints for many traits that appear to separate continental samples well; however, it is likely that dichotomizing traits results in loss of information that may be valuable in other comparisons. For example, LM2CN is present in 100 percent of individuals across groups when dichotomized according to the traditional breakpoint; as such, it is not useful in discriminating among groups. However, frequencies of four, five, and six cusps do vary; thus, the trait is informative when not dichotomized. Intergroup variation is necessary to evaluate relationships in traditional studies, but in a forensic

context, classification, rather than establishing group relationships, is the goal. For the current research, we utilized statistical classification methods that work with both dichotomous and polychotomous data.

20.4.2 Statistical classification methods

For some classification methods (described later), principal components analysis (PCA) was first used to reduce the number of variables and normalize the data. PCA creates new independent linear combinations of original scores that explain variation in the original variables through accommodating trait correlations. In this way, the data are normalized and fewer uncorrelated principal components can explain more of the variation.

Scores for each trait were analyzed using several multivariate classification methods; each generally takes correlations among variables into account, provides estimated accuracy rates, and has different requirements for optimal classification accuracy of individuals, though multivariate normality is an assumption of most methods. Discriminant function analysis is a parametric statistic that maximizes among-group variation through a linear combination of weights used to classify a new individual into one of the reference groups based on Mahalanobis distance from group means (Tabachnick and Fidell 2001). Discriminant methods make intuitive sense because an individual will be classified into the group to which it is most similar. Linear discriminant function analysis (LDFA) is the best-known discriminant technique and classifies best when the level of variation is more or less the same in all groups. When the latter is not true, quadratic discriminant function analysis (QDFA) can be used; however, classification accuracy often suffers compared to that of LDFA, and sample size requirements are higher. Both discriminant methods depend on another requirement: that is, the discriminant scores are more or less normally distributed; a normal distribution is likely the case when the original data are normally distributed. In the case of binary and ordinal data, data can be normalized by converting them to principal component scores (see previous discussion). Another option is a semiparametric method known as logistic regression (LR), which directly estimates probabilities of group membership and has fewer requirements than DFA. For instance, levels of variation among groups can differ, the data need not be normally distributed, and, in fact, the data can be categorical, continuous, or both.

Two additional methods of statistical classification are termed nonparametric because they use individual rather than group similarities for classification. K-nearest neighbor analysis (k-NN) classifies unknown individuals on the basis of the k most similar reference individuals in samples, often using a

majority rule; for example, if the three most similar individuals to an unknown individual are two males and a female, then the k-NN method would classify the unknown as a male. Kernel probability density (KPD) classifies unknown individuals using a probability density function calculated from reference individuals. An unknown individual is classified into the reference group with the highest cumulative probability based on the observations.

Newer classification methods depend on the power of computers a great deal more and are generally called "machine learning" methods. They include decision trees, random forests, and support vector machines, which are in part "black box" classifiers that do not work directly with group parameters, but rather experiment with a large number of ways of separating groups of individuals and manipulating observations in the sample (Williams 2011). Decision trees are also known as classification and regression trees and employ a sequential series of rules to estimate group membership starting with the most effective rule (a "node") that separates individuals into two or more subsamples most accurately according to group membership. For instance, one rule could be "LP1LC <= 4," which would divide the entire sample into two "branches," one that shows greater lower anterior premolar lingual cusp complexity and one that does not (if that rule were the most effective at dividing the total sample into the original groups). Further nodes continue to divide the branches, sometimes using rules that split a branch into more than two parts, until the divisions cannot be separated any better to reflect the original groups.

Random forests classification uses many random subsets of the variables and resamplings of the original data to produce hundreds of decision trees, called an ensemble; the consensus of the ensemble is used to determine the best classification rules. Random forests can generally tolerate many variables simultaneously, even "noisy" ones. Support vector machine classification identifies boundaries between individuals that lie near boundaries separating groups; it then manipulates the data to produce the optimal linear boundaries that best separate those individuals from different groups. Support vector machines can classify especially well when there are many variables with nonlinear relationships to each other. However, there are many possible data transformations to choose from and each influences classification accuracy.

In evaluating statistical classification functions, the most important measure is the correct classification rate, which is estimated from the reference samples because estimates of accuracy are biased when the same individuals are evaluated and, in a reference group, all methods incorporate cross-validation. The most widely used method of cross-validation in traditional classification methods is leave-one-out-cross-validation (LOOCV; Lachenbruch and Mickey 1968). In LOOCV, each individual in the total reference sample is sequentially

removed, and classification procedures are followed using the rest of the sample and applied to the removed individual. The accuracy rate is tabulated from the way each removed individual is classified. Logistic regression classification accuracy is often based on an algorithm and can be biased optimistically (Peng and So 2002). Machine learning classifiers divide the total sample into a training sample to derive the best rules for classification and then apply them to a holdout, or validation sample, usually between 10 percent and 25 percent of the total sample. For these results, 30 percent of the total sample was used to estimate classification accuracy. Additionally, there are many settings that can be adjusted to influence performance, and further experimentation is needed; the results presented here represent the most widely used default settings (Williams 2011). Machine learning methods must employ a more rigorous kind of cross-validation because they otherwise report optimistically biased results. They need somewhat larger sample sizes to arrive at the most accurate classifications.

The overall correct classification rate and classification rates for each group are important, but so are the group misclassification percentages. Some groups classify at higher rates than others, and some tend to be misclassified into specific groups. In multigroup analyses, some groups are often more similar to one another than other groups; as such, maximizing correct classification is challenging. An additional challenge results from the fact that, oftentimes, the use of fewer variables will classify reference groups better than more, as a result of overfitting data (i.e., too many variables relative to individuals), or because some variables do not differ among groups. Stepwise selection methods often identify the best variables to use in classification. Fordisc 3.0 (Ousley and Jantz 2005), R (R Development Core Team 2011), SAS version 9.0 (SAS Institute, 2002), and SYSTAT for Windows version 13 (Systat Software, 2009) were used for all statistical analyses.

20.5 Results

The distance matrices based on LDFA of the principal components of binary and ordinal variables for all group combinations are shown in Table 20.3. There are six tables, one based on binary and one based on ordinal data for each of three different group comparisons. The first set of two tables shows results comparing six potentially different race groups. The second set leaves out NA and AsA samples and only compares AfA, EuA, and the two separate Hispanic American samples. The third set compares AfA, EuA, and a combined Hispanic American sample. We ran these particular combinations as they are of traditional interest in forensic studies.

Table 20.3. *Distance matrices of principal components based on linear discriminant function analysis*

Six groups						
	AfA	AsA	EA	HSE	HW	NA
AfA	–	*9.1*	*4.8*	*6.6*	*8.3*	*22.3*
AsA	7.6	–	*8.0*	*4.6*	*2.5*	*7.5*
EA	5.0	8.3	–	*6.0*	*5.9*	*21.1*
HSE	6.7	3.5	7.1	–	*1.4*	*11.4*
HW	7.2	1.8	7.3	1.2	–	*8.4*
NA	14.4	6.1	15.1	8.0	6.3	–
Four groups						
	AfA	EA	HSE	HW		
AfA	–	*4.7*	*6.6*	*8.0*		
EA	4.6	–	*6.1*	*5.8*		
HSE	6.6	7.0	–	*1.8*		
HW	6.9	7.3	1.3	–		
Three groups						
	AfA	EA	Hispanic			
AfA	–	*4.5*	*6.7*			
EA	4.8	–	*5.4*			
Hispanic	6.6	6.9	–			

Note: Results based on dichotomized data are below the diagonal. Results based on ordinal data are above the diagonal and in italics.

A distance matrix provides one number that represents intergroup differences when the variation in all groups is the same, but the data from these groups showed significant heterogeneity in their variance-covariance matrices, so the distances shown are only roughly comparable. The six-group matrices are similar. The NA sample shows the highest distances from all other groups and is the outlying group in the dendrogram (Figure 20.1). Some unexpected results are apparent: On the basis of distances, the AfA sample is most similar to EuA and is roughly as different from HSE sample as HAW, despite evidence for more genetic input from African and recent African-derived populations (Bertoni et al. 2,003). The AsA sample is most similar to HW and more differentiated from the NA, despite the fact that the NA sample consists of Navajo and Pima, both presently in the Southwest United States. Finally, the HW sample is most similar to the HASE sample and as roughly equidistant from NA (6.3), EuA (7.3), and AfA (7.2) using binary variables but is more similar to EuA (5.9) than to NA (8.4) using ordinal variables.

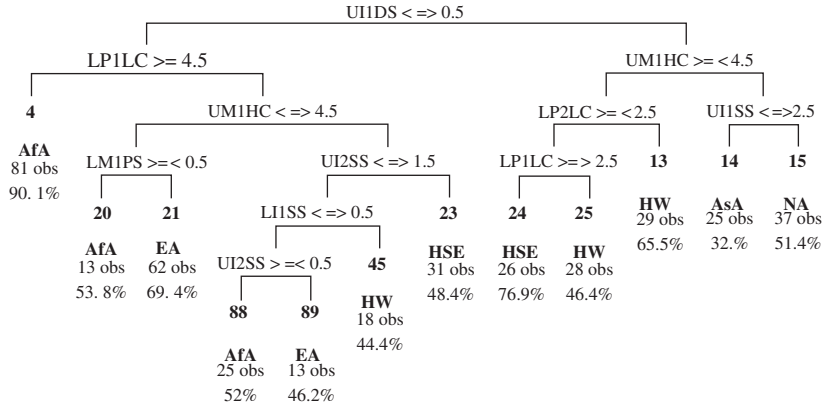

Figure 20.1. A decision tree built using dental morphology traits. We can follow the decisions by observing the branches corresponding to the tests at each node. The **< =>** notation on the root (top) node indicates that we branch left if UI1DS is 0 and branch right if it is greater than or equal to 1. The terminal (leaf) nodes include a node number for reference, the group that the node is identifying, the number of training observations at the node, and the strength or confidence of the decision.

Classification results using LDFA, QDFA, Kernel, k-NN, and logistic regression methods with binary and ordinal variables are shown in Table 20.4, with the binary and ordinal classification results for the same group combinations as in the distance matrices. In the classification matrices, the percentages of each group in the leftmost column are given in the group column into which they were classified, and the correct percentage by group is on the diagonal, in bold, as are any classification percentages higher than those on the diagonal. In many ways the classification results mirror the distance matrices. One major difference is that the most unique sample as far as traditional classifications are concerned is the EuA sample, which shows the highest classification accuracy in nearly every comparison and method. This is somewhat surprising, because in the distance matrices, the NA was the most differentiated sample. However, the data were not normally distributed and the distances are approximations.

The classification matrices are on the whole similar, no matter what method was used, though classification accuracy is expected to increase as fewer groups are being classified. In the six group analyses, overall classification accuracy ranges between 45 percent and 72 percent; for the four group classification, they range from 52 percent to 77 percent; the three group classifications ranged from 65 percent to 84 percent correctly classified. In nearly all classifications, there were large disparities between the highest classification percentages and the lowest, meaning that different score distributions within groups could not be compensated for by any method. On the whole, the AsA sample had the

Table 20.4. *Classification results of linear discriminant function, quadratic discriminant function, kernal probability, and k-nearest neighbor analyses*

Six groups

Binary

	LDFA (56%)					
	AfA	AsA	EA	HSE	HW	NA
AfA	**72**	7	11	5	5	0
AsA	4	**44**	4	7	15	26
EA	14	5	**75**	3	3	0
HSE	12	9	8	**38**	19	14
HW	6	21	14	21	**24**	14
NA	0	16	0	11	5	**68**

	QDFA (45%)					
	AfA	AsA	EA	HSE	HW	NA
AfA	**44**	7	40	5	5	0
AsA	0	**33**	7	15	33	11
EA	9	2	**86**	1	3	0
HSE	10	*24*	13	**26**	22	5
HW	10	*34*	14	18	**18**	6
NA	0	*32*	0	21	21	**26**

	Kernel (53%)					
	AfA	AsA	EA	HSE	HW	NA
AfA	**59**	3	35	2	1	0
AsA	0	**30**	*33*	4	7	26
EA	10	1	**89**	0	0	0
HSE	13	5	*29*	**26**	13	14
HW	4	7	*32*	10	**24**	23
NA	0	11	0	0	11	**79**

	kNN (56%)					
	AfA	AsA	EA	HSE	HW	NA
AfA	**74**	6	11	3	4	2
AsA	3	**38**	3	14	10	31
EA	14	3	**78**	3	3	0
HSE	14	14	14	**32**	8	17
HW	8	*25*	15	12	**21**	19
NA	0	4	0	7	11	**78**

	Logistic (64%)					
	AfA	AsA	EA	HSE	HW	NA
AfA	**77**	3	7	8	5	0
AsA	15	**26**	0	22	*26*	11
EA	18	0	**78**	1	3	0
HSE	9	4	6	**55**	21	5
HW	6	7	13	27	**44**	4
NA	5	5	0	11	16	**63**

Ordinal

	LDFA (59%)					
	AfA	AsA	EA	HSE	HW	NA
AfA	**71**	3	13	7	5	0
AsA	0	**44**	4	11	22	19
EA	7	6	**81**	2	5	0
HSE	12	8	10	**41**	22	8
HW	1	18	15	20	**30**	15
NA	0	21	5	5	0	**68**

	QDFA (56%)					
	AfA	AsA	EA	HSE	HW	NA
AfA	**65**	2	24	6	3	0
AsA	7	**15**	4	15	*56*	4
EA	5	1	**81**	5	9	0
HSE	13	6	12	**45**	24	0
HW	6	17	10	*27*	**39**	1
NA	5	11	0	21	*42*	**21**

	Kernel (50%)					
	AfA	AsA	EA	HSE	HW	NA
AfA	**44**	2	51	2	1	1
AsA	0	**22**	*44*	0	26	**7**
EA	0	1	**99**	0	0	0
HSE	6	4	*54*	**14**	19	3
HW	0	10	*49*	1	**34**	6
NA	0	16	5	0	11	**68**

	kNN (55%)					
	AfA	AsA	EA	HSE	HW	NA
AfA	**56**	8	25	6	3	3
AsA	0	**48**	7	7	26	11
EA	3	3	**86**	3	6	0
HSE	6	12	19	**33**	22	8
HW	0	20	15	14	**35**	15
NA	0	21	0	5	26	**47**

	Logistic (72%)					
	AfA	AsA	EA	HSE	HW	NA
AfA	**79**	1	12	4	4	0
AsA	6	**66**	2	10	15	0
EA	16	1	**76**	5	3	0
HSE	13	3	8	**57**	19	0
HW	9	4	6	16	**65**	0
NA	0	0	0	0	0	**100**

Table 20.4. (*cont.*)

Four groups

Binary					**Ordinal**				
	LDFA (64%)				LDFA (70%)				
	AfA	EA	HSE	HW		AfA	EA	HSE	HW
AfA	**71**	11	8	9	AfA	**71**	16	8	5
EA	16	**76**	4	4	EA	9	**86**	4	2
HSE	14	9	**47**	**29**	HSE	10	12	**54**	24
HW	6	13	**31**	**51**	HW	3	15	24	**58**
	QDFA (60%)					QDFA (63%)			
	AfA	EA	HSE	HW		AfA	EA	HSE	HW
AfA	**61**	23	7	9	AfA	**64**	24	9	3
EA	13	**80**	3	4	EA	11	**80**	1	9
HSE	13	9	**45**	33	HSE	19	12	**40**	29
HW	13	13	30	**45**	HW	7	11	23	**59**
	Kernel (60%)				Kernel (52%)				
	AfA	EA	HSE	HW		AfA	EA	HSE	HW
AfA	**59**	34	3	3	AfA	**42**	55	2	1
EA	7	**93**	0	0	EA	1	**99**	0	0
HSE	13	32	**35**	21	HSE	6	*59*	**14**	21
HW	7	34	20	**39**	HW	1	*58*	1	**39**
	kNN (64%)				kNN (64%)				
	AfA	EA	HSE	HW		AfA	EA	HSE	HW
AfA	**70**	12	10	8	AfA	**56**	23	13	8
EA	15	**77**	4	4	EA	8	**85**	4	4
HSE	12	12	**54**	23	HSE	6	15	**49**	29
HW	7	14	34	**45**	HW	4	18	21	**56**
	Logistic (70%)				Logistic (77%)				
	AfA	EA	HSE	HW		AfA	EA	HSE	HW
AFR	**76**	11	6	7	AfA	**78**	10	7	5
EA	12	**80**	4	4	EA	12	**83**	4	1
HSE	7	10	**53**	30	HSE	6	10	**65**	19
HW	6	10	16	**68**	HW	4	4	11	**81**

Three groups

Binary				**Ordinal**			
	LDFA (76%)			LDFA (78%)			
	AfA	EA	Hispanic		AfA	EA	Hispanic
AfA	**75**	14	11	AfA	**76**	13	10
EA	16	**78**	6	EA	10	**85**	6
Hispanic	11	13	**76**	Hispanic	8	17	**75**

(*continued*)

Table 20.4. (*cont.*)

Three groups

Binary				**Ordinal**			
	QDFA (72%)			QDFA (74%)			
	AfA	EA	Hispanic		AfA	EA	Hispanic
AfA	**63**	23	14	AfA	**66**	21	13
EA	15	**76**	9	EA	7	**84**	10
Hispanic	15	10	**75**	Hispanic	11	15	**75**
	Kernel (67%)				Kernel (65%)		
	AfA	EA	Hispanic		AfA	EA	Hispanic
AfA	**63**	33	4	AfA	**50**	46	4
EA	7	**93**	0	EA	0	**99**	1
Hispanic	13	36	**51**	Hispanic	5	42	**54**
	kNN (71%)				kNN (74%)		
	AfA	EA	Hispanic		AfA	EA	Hispanic
AfA	**71**	19	9	AfA	**61**	18	20
EA	16	**81**	3	EA	5	**84**	12
Hispanic	15	21	**64**	Hispanic	7	15	**78**
	Logistic (82%)				Logistic (84%)		
	AfA	EA	Hispanic		AfA	EA	Hispanic
AfA	**74**	9	17	AfA	**77**	10	13
EA	11	**79**	9	EA	10	**84**	6
Hispanic	6	8	**86**	Hispanic	4	7	**88**

Note: Correct classification frequencies are in bold. Cases where incorrect classification frequencies are at least as large as correct classifications are in italics.

greatest number of misclassifications, usually into the Hispanic groups or NAs. Oddly enough, the kernel and k-NN classification matrices repeat a pattern discerned in the distance matrices, that the HAW sample shows similarities to the EuA sample, with more HAW individuals classified into EuA than to their own group, paralleling recent findings that Hispanics from the Southwest average 60–70 percent European admixture (Bonilla et al. 2004; unpublished research).

In comparing the classifications described previously, logistic regression performed best, and analyzing ordinal scores improved classification accuracy. These results likely reflect the fact that logistic regression makes fewer distributional assumptions about the data: the data can be continuous, categorical, and ordinal, or a combination of the three, and different levels of variation can be present in groups. The ordinal scores likely improved classifications using all methods because they contain more information and the groups varied

more in their ordinal scores. Also, converting the original scores, both binary and ordinal, to principal components, while necessary for the traditional/linear methods (LDFA, QDFA, k-NN, kernel), actually decreased accuracy when using logistic regression. When classifying, it is best to use the most appropriate method based on the goals of the analysis and the nature of the data at hand, rather than preconditioning or transforming observations (through calculating principal components or converting to binary values) to use easier or more familiar methods that have specific requirements. The high performance of logistic regression should come as no surprise because it has fewer assumptions to violate; however, estimated classification accuracy is likely somewhat positively biased. The generally good performance of LDFA is surprising given that one of the assumptions necessary for its optimal classification (homogeneity of variance-covariance matrices) was violated, and the other classification methods do not have that requirement.

Most of the machine learning methods of classification did not perform as well as the traditional methods but echo the finding that analyzing ordinal data produces higher classification accuracies than analyzing dichotomous data. Some of the lower classification rates may be due to more rigorous cross-validation, because the calculated classifications are tested on a completely independent part of the total sample. Table 20.5 shows classification matrices for the six-group and three-group classifications using both dichotomous and ordinal observations. Once again, classification accuracies were greater using ordinal data, though the estimated accuracies were lower than using traditional methods. The exception is the three-way random forest method classification accuracy, which was nearly as high (83 percent) as the three-way logistic regression classification (84 percent). However, the three-way random forest classification also showed a large difference between the highest classification accuracy (92 percent) and the lowest classification accuracy (71 percent). Indeed, all methods showed rather large discrepancies between the highest and lowest percentages, often because the AsA sample generally classified poorly, but also because AfA were often misclassified into the EA or Hispanic groups.

20.6 Discussion

The usual goal of dental morphological analysis is improving our understanding of population relationships at both small and large scales. This goal is different from the application presented here, the classification of unknown individuals into known groups. However, these two types of analyses are intimately linked, as they draw on the same phenomenon, a correlation between

Table 20.5. *Classification results of three machine learning approaches: decision trees, random forests, and support vector machine*

Six groups	Dichotomous						Ordinal						
	Decision tree (41%)							Decision tree (55%)					
	AfA	AsA	EA	HSE	HW	NA		AfA	AsA	EA	HSE	HW	NA
AfA	**79**	0	7	6	6	1	AfA	**64**	0	16	12	9	0
AsA	10	**0**	10	7	41	14	AsA	6	**0**	13	*31*	*44*	6
EA	34	0	**60**	6	0	0	EA	10	0	**79**	10	0	0
HSE	16	0	7	**29**	39	7	HSE	12	0	12	**64**	10	2
HW	25	0	5	26	**23**	16	HW	3	0	13	*50*	**30**	3
NA	4	0	0	4	12	**36**	NA	25	0	0	13	0	**63**
	Random forests (48%)							Random forests (66%)					
	AfA	AsA	EA	HSE	HW	NA		AfA	AsA	EA	HSE	HW	NA
AfA	**78**	0	13	3	6	0	AfA	**80**	2	5	7	5	0
AsA	*18*	**9**	*18*	9	*36*	0	AsA	0	**8**	0	0	83	8
EA	31	0	**62**	5	3	0	EA	13	4	**74**	9	0	0
HSE	3	0	10	**38**	41	3	HSE	10	0	13	**57**	20	0
HW	*25*	3	9	22	**25**	9	HW	5	0	5	5	**71**	14
NA	13	0	0	0	0	**38**	NA	0	0	0	0	20	**80**
	Support vector machine (51%)							Support vector machine (64%)					
	AfA	AsA	EA	HSE	HW	NA		AfA	AsA	EA	HSE	HW	NA
AfA	**69**	0	22	6	3	0	AfA	**73**	0	7	15	5	0
AsA	*40*	**0**	0	10	*50*	0	AsA	0	**0**	0	*25*	*67*	8
EA	28	0	**64**	3	5	0	EA	9	0	**74**	4	13	0
HSE	11	0	11	**43**	36	0	HSE	10	0	13	**67**	10	0
HW	20	0	17	17	**43**	3	HW	5	0	0	19	**71**	5
NA	25	0	0	0	50	**25**	NA	0	0	0	*40*	20	**40**
Three groups	Decision tree (77%)							Decision tree (72%)					
	AfA	EA	Hispanic					AfA	EA	Hispanic			
AfA	**67**	9	24				AfA	**60**	12	28			
EA	15	**55**	30				EA	10	**66**	24			
Hispanic	8	4	**89**				Hispanic	8	8	**83**			
	Random forests (74%)							Random forests (83%)					
	AfA	EA	Hispanic					AfA	EA	Hispanic			
AfA	**59**	18	23				AfA	**71**	0	29			
EA	15	**64**	21				EA	11	**83**	6			
Hispanic	10	3	**86**				Hispanic	0	8	**92**			
	Support vector machine (71%)							Support vector machine (79%)					
	AfA	EA	Hispanic					AfA	EA	Hispanic			
AfA	**59**	18	23				AfA	**65**	0	35			
EA	18	**64**	18				EA	6	**83**	11			
Hispanic	10	10	**79**				Hispanic	0	11	**89**			

Note: Correct classification frequencies are in bold. Cases where incorrect classification frequencies are at least as large as correct classifications are in italics.

recognizable groups and biological characteristics of these groups, due to the groups' evolutionary histories. Because these two studies draw on the same data, resulting from the same phenomena, each can inform the other.

This chapter presents one of the first uses of multivariate statistical techniques to analyze dental morphological data to estimate race. It is the first to apply machine learning techniques to both dental characteristics and the classification of race for forensic purposes (although the potential value of machine learning techniques in forensics has been previously investigated; see Mena 2012). Further experimentation with machine learning techniques should produce improvements in classification, although supplementing future analyses with additional dental morphological variants may be necessary as well.

An interesting point of consideration is whether it is important to include Hispanic Americans from various areas of the United States when classifying remains. It is generally known, and supported by genetic evidence, that Hispanics in the southeastern United States, such as the Floridian sample included here, have African ancestry as an important component of their genetic heritage. Moreover, African ancestry is much lower in Hispanics in the U.S. West, such as our New Mexican and Californian samples. However, distances between HSE and HW are the smallest among the groups. All classification techniques in this study had their lowest success discriminating among groups with at least some Asian or Asian-derived ancestry: AsA, HSE, HW, and NA. The sources (African or European) and quantities of other admixture in these groups seem of reduced importance in the configuration of dental characters an individual is likely to have. This may reflect dominance of the alleles associated with traits such as shoveling that are commonly associated with Asian and Asian-derived groups. If so, one Hispanic sample may be as useful as any other for developing classification methods that can apply across the country. Unfortunately, classification success may be low when attempting to distinguish between Hispanics and other partially Asian-derived groups, such as Native Americans or Asian Americans. While these groups are considered different races in social contexts, they may not be especially different dentally. If this is true, it is an important consideration in any study of biological distance that includes admixture with these groups.

Using multivariate statistical approaches to dental morphology greatly increases accuracy compared to the use of one or two traits, such as Carabelli's trait and shovel-shaped incisors, alone. Additionally, converting the expression of traits through dichotomizing reduces the trait variation among groups. There seems little justification for dichotomization in traits if multistate traits can be recorded consistently (Nichol and Turner 1986).

Compared to other published research, our three-way random forest (84 percent) and logistic regression (83 percent) analyses produced classification

accuracies that are a bit lower than the 89.5 percent reported by Hefner (2011) using random forest classification and 88.7 percent using k-NN analysis (Hefner et al. 2012) using a combination of metric and nonmetric observations in crania from the same three groups. While our analyses often showed classification bias, with certain groups being classified more accurately than others, Hefner reported little or no bias in his classification results. Because teeth often survive taphonomic events that skulls do not, it behooves future researchers to improve the accuracy of race classification, at least to the level of cranial data.

Dental morphological data, combined with advanced statistical techniques, have great potential for forensic estimation of race. Not surprisingly, these methods produce more accurate classifications for some groups than for others. These variable success rates result from a number of factors, including sampling issues, but likely also reflect real similarities and differences among several of the groups in the frequencies and expressions of dental morphological traits.

Appendix *Trait sample sizes, dichotomized frequencies, and grade frequencies for each group*

Trait	n	Dichotomous frequency	AfA									
			0	1	2	3	4	5	6	7	8	9
WING	243	0.02		0.024	0.029	0.866	0.081					
UI1LC	259	0.20	0.427	0.378	0.160	0.036						
UI1SS	256	0.08	0.288	0.392	0.243	0.072	0.005					
UI2SS	259	0.35	0.183	0.451	0.277	0.080	0.004	0.004				
UCSS	249	0.24	0.178	0.570	0.229	0.023						
UI1DS	258	0.02	0.951	0.036	0.004	0.009						
UI2DS	260	0.03	0.973	0.022		0.004						
UP1AC	249	0.26	0.734	0.070	0.145	0.051						
UM1MC	256	0.60				0.014	0.434	0.529	0.023			
UM1HC	254	0.44	0.005			0.046	0.566	0.356	0.027			
UM1C5	244	0.37	0.675	0.177	0.115	0.029	0.005					
LI1SS	257	0.22	0.780	0.206	0.013							
LI2SS	261	0.24	0.767	0.229	0.004							
LP1LC	254	0.66	0.018	0.110	0.087	0.132	0.064	0.178	0.068	0.237	0.078	0.027
LP2LC	256	0.96		0.041	0.063	0.136	0.154	0.054	0.235	0.113	0.059	0.145
LM1GP	107	0.68	0.325	0.602	0.072							
LM2GP	110	0.56	0.154	0.582	0.264							
LM2CN	185	1.00					0.395	0.493	0.112			
LM1PS	225	0.19	0.800	0.189	0.005					0.005		
LM2PS	209	0.09	0.920	0.069	0.011							
LM1TC	188	0.20	0.846	0.154								
LM2C7	210	0.27	0.777	0.097	0.069	0.040	0.017					

Appendix (*cont.*)

			AsA									
Trait	n		0	1	2	3	4	5	6	7	8	9
WING	60	0.08		0.083	0.117	0.733	0.067					
UI1LC	68	0.06	0.632	0.309	0.044	0.015						
UI1SS	67	0.43	0.030	0.119	0.403	0.358	0.090					
UI2SS	66	0.91	0.030	0.045	0.348	0.455	0.106	0.015				
UCSS	62	0.66	0.097	0.226	0.565	0.113						
UI1DS	67	0.37	0.313	0.299	0.239	0.119	0.030					
UI2DS	66	0.44	0.545	0.303	0.136		0.015					
UP1AC	59	0.64	0.339	0.322	0.085	0.254						
UM1MC	66	0.73					0.258	0.697	0.045			
UM1HC	67	0.60				0.015	0.388	0.537	0.060			
UM1C5	61	0.34	0.656	0.115	0.180	0.049						
LI1SS	67	0.66	0.328	0.463	0.194	0.015						
LI2SS	70	0.59	0.414	0.443	0.114	0.029						
LP1LC	66	0.09	0.091	0.273	0.273	0.273	0.030	0.015	0.030		0.015	
LP2LC	67	0.87		0.134	0.164	0.433	0.194		0.015		0.060	
LM1GP	22	0.00	0.957		0.043							
LM2GP	26	0.15	0.296	0.148	0.556							
LM2CN	54	1.00					0.444	0.407	0.148			
LM1PS	63	0.60	0.397	0.571	0.016			0.016				
LM2PS	59	0.19	0.814	0.169						0.017		
LM1TC	47	0.13	0.872	0.128								
LM2C7	52	0.06	0.943	0.057								

			EA									
Trait	n		0	1	2	3	4	5	6	7	8	9
WING	147	0.01		0.014		0.803	0.184					
UI1LC	155	0.13	0.548	0.323	0.103	0.026						
UI1SS	154	0.01	0.338	0.500	0.156	0.006						
UI2SS	152	0.14	0.346	0.516	0.137							
UCSS	151	0.04	0.523	0.437	0.040							
UI1DS	155	0.00	0.987	0.013								
UI2DS	153	0.01	0.993	0.007								
UP1AC	150	0.17	0.833	0.033	0.087	0.047						
UM1MC	155	0.42			0.006		0.581	0.406	0.006			
UM1HC	153	0.28				0.026	0.693	0.255	0.026			
UM1C5	150	0.15	0.853	0.087	0.060							
LI1SS	153	0.18	0.824	0.176								
LI2SS	154	0.12	0.870	0.130								
LP1LC	149	0.11	0.047	0.282	0.242	0.322	0.047	0.054		0.007		
LP2LC	150	0.79	0.020	0.187	0.147	0.260	0.227	0.067	0.027	0.053	0.013	
LM1GP	61	0.95		0.967	0.033							
LM2GP	66	0.52		0.523	0.477							
LM2CN	130	1.00					0.792	0.185	0.023			
LM1PS	148	0.04	0.959	0.041								
LM2PS	143	0.02	0.979	0.021								
LM1TC	125	0.01	0.992	0.008								
LM2C7	139	0.06	0.935	0.058	0.007							

(*continued*)

Appendix (*cont.*)

			HASE									
Trait	n		0	1	2	3	4	5	6	7	8	9
WING	183	0.03		0.033	0.033	0.803	0.131					
UI1LC	197	0.22	0.299	0.487	0.183	0.030						
UI1SS	194	0.26	0.077	0.314	0.345	0.170	0.062	0.031				
UI2SS	189	0.63	0.048	0.324	0.410	0.154	0.053	0.011				
UCSS	174	0.45	0.075	0.477	0.345	0.103						
UI1DS	195	0.33	0.410	0.262	0.138	0.082	0.067	0.041				
UI2DS	192	0.55	0.453	0.328	0.141	0.063	0.016					
UP1AC	174	0.47	0.529	0.155	0.190	0.126						
UM1MC	197	0.89					0.107	0.812	0.081			
UM1HC	192	0.83	0.005	0.005		0.005	0.156	0.693	0.135			
UM1C5	174	0.48	0.523	0.241	0.172	0.057		0.006				
LI1SS	196	0.62	0.383	0.464	0.133	0.020						
LI2SS	198	0.65	0.359	0.500	0.136	0.005						
LP1LC	195	0.16	0.041	0.369	0.103	0.328	0.051	0.056	0.026	0.010	0.010	0.005
LP2LC	188	0.87		0.128	0.064	0.346	0.181	0.069	0.037	0.085	0.064	0.027
LM1GP	70	0.04	0.901	0.042	0.056							
LM2GP	89	0.07	0.500	0.067	0.433							
LM2CN	141	1.00					0.709	0.241	0.050			
LM1PS	188	0.29	0.713	0.250	0.011	0.011	0.005	0.005	0.005			
LM2PS	173	0.13	0.873	0.098		0.006	0.012	0.006		0.006		
LM1TC	160	0.11	0.888	0.113								
LM2C7	156	0.49	0.506	0.327	0.147	0.019						

			HAW									
Trait	n		0	1	2	3	4	5	6	7	8	9
WING	182	0.16		0.122	0.050	0.748	0.079					
UI1LC	223	0.17	0.480	0.364	0.150	0.006						
UI1SS	224	0.32	0.086	0.305	0.356	0.178	0.057	0.017				
UI2SS	216	0.65	0.078	0.289	0.398	0.181	0.048			0.006		
UCSS	194	0.38	0.114	0.450	0.396	0.040						
UI1DS	222	0.30	0.407	0.349	0.151	0.070	0.023					
UI2DS	216	0.50	0.602	0.283	0.108	0.006						
UP1AC	212	0.34	0.611	0.099	0.198	0.093						
UM1MC	223	0.87					0.145	0.809	0.046			
UM1HC	223	0.77	0.006			0.006	0.237	0.630	0.121			
UM1C5	218	0.42	0.649	0.161	0.155	0.030	0.006					
LI1SS	216	0.61	0.345	0.444	0.211							
LI2SS	221	0.63	0.329	0.486	0.185							
LP1LC	219	0.08	0.095	0.420	0.249	0.160	0.012	0.047	0.012	0.006		
LP2LC	215	0.67		0.257	0.186	0.323	0.078	0.066	0.018	0.012	0.048	0.012
LM1GP	90	0.09	0.955	0.030	0.015							
LM2GP	98	0.34	0.433	0.119	0.448							
LM2CN	165	1.00					0.648	0.295	0.057			
LM1PS	212	0.50	0.472	0.509	0.012		0.006					
LM2PS	187	0.17	0.817	0.176					0.007			
LM1TC	170	0.08	0.923	0.077								
LM2C7	182	0.10	0.883	0.095	0.022							

Appendix (*cont.*)

			NA									
Trait	n		0	1	2	3	4	5	6	7	8	9
WING	60	0.27		0.267	0.150	0.583						
UI1LC	61	0.03	0.574	0.393	0.033							
UI1SS	61	0.85			0.148	0.410	0.279	0.131	0.016	0.016		
UI2SS	58	1.00			0.172	0.414	0.259	0.138		0.017		
UCSS	52	0.94		0.058	0.365	0.500	0.077					
UI1DS	60	0.72	0.117	0.167	0.200	0.250	0.183	0.067	0.017			
UI2DS	58	0.74	0.259	0.172	0.362	0.172	0.034					
UP1AC	55	0.58	0.418	0.036	0.273	0.273						
UM1MC	61	0.74				0.016	0.246	0.705	0.033			
UM1HC	61	0.21				0.033	0.754	0.213				
UM1C5	58	0.47	0.534	0.259	0.121	0.052	0.017	0.017				
LI1SS	51	1.00		0.275	0.588	0.137						
LI2SS	50	1.00		0.180	0.720	0.100						
LP1LC	58	0.02	0.121	0.483	0.190	0.190	0.017					
LP2LC	59	0.64		0.356	0.153	0.186	0.119	0.085	0.051	0.051		
LM1GP	18	0.28		0.278	0.722							
LM2GP	15	0.87		0.867	0.133							
LM2CN	40	1.00					0.200	0.550	0.250			
LM1PS	56	0.39	0.607	0.321	0.036			0.018	0.018			
LM2PS	57	0.19	0.807	0.140	0.053							
LM1TC	41	0.20	0.805	0.195								
LM2C7	53	0.13	0.868	0.113	0.019							

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21 *Wear's the problem? Examining the effect of dental wear on studies of crown morphology*

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21.1 Introduction

The purpose of this chapter is to build upon previous research (Burnett 1998) that investigated the effect(s) of dental wear on scoring dental morphological traits. Specifically, on the basis of results from the study of an archaeologically derived dental sample by two observers with differing levels of trait recording experience, we address three questions: (1) Are different traits affected by dental wear in the same manner? (2) Do wear biases affect individual researchers differently? and (3) What are the causes of wear-related scoring biases?

21.2 Dental wear

One downside to the study of teeth is the progressive loss of crown surface, and hence biological information, due to various endogenous and exogenous sources following eruption. Dental wear results from three primary sources: attrition, abrasion, and erosion (Kaidonis 2008). Attrition results from occlusal contact between isomeres and interproximal contact between adjacent teeth. It can result from both functional occlusion and parafunctional activities, including bruxism. Attrition manifests as well-defined, flat-planed opposing facets with parallel striations (Kaidonis 2008).

Abrasion results from friction between teeth and items or substances introduced into the mouth. Abrasion from dietary items may include non–spatially specific wear from mastication, but also potential localized wear from specific

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food processing (e.g., Irish and Turner 1987, 1997; Turner and Machado 1983). Examples of nondietary causes of abrasion include grit in the diet, materials for dental hygiene including toothbrushes and toothpicks (Bergstrom and Lavstedt 1979; Frayer 1991; Ungar et al. 2001), and task-related behaviors (Erdal 2008; Larsen 1985; Turner and Anderson 2003).

Lastly, erosion is defined as the chemical dissolution of dental tissues in the absence of plaque, which appears to be a largely modern phenomenon (Kaidonis 2008). Causes of erosion include vomiting due to alcoholism or eating disorders, highly acidic foods or beverages, and inhalation of acidic fumes in industrial contexts (Holbrook and Árnadóttir 2003; Kaidonis 2008; Pindborg 1970). In reality, attrition, abrasion, and erosion rarely occur in isolation. In nonindustrialized societies, attrition and abrasion likely acted in concert on the dentition as primary forces, while the softness of the modern diet has moderated the effects of abrasion. However, demineralization from acidic food and beverages has increased the susceptibility of tooth enamel to both attrition and abrasion (Khan and Young 2011).

The study of dental wear is complex in and of itself since the effects increase with age (e.g., Molnar 1971; Moorrees 1957; Tomenchuk and Mayhall 1979), may differ between sexes (Molnar 1971; Tomenchuk and Mayhall 1979), and can vary over time in the same population (Kaifu 1999; Moorrees 1957). Patterns and degree of wear also differ by diet (Hartney 1981; Hinton 1981; Smith 1984). For example, wear level by age varies considerably between Greenlanders retaining a traditional diet and those adopting a European diet (Davies and Pederson 1955). Modern foods generally result in less wear, though erosion is more of a factor (Kaidonis 2008). Idiosyncratic behaviors (pen/nail chewing, toothpick grooves, pipe facets, etc.) also have an effect (Johansson et al. 1991). In the remainder of this chapter we do not differentiate among attrition, abrasion, and erosion – because the end result is the same, that is, loss of crown surface. Thus, for simplicity, the generic term "dental wear" is used.

21.3 The result(s) of tooth wear

The confounding effect of wear on studies of crown morphology has long been known, since it progressively removes surface details even at light to moderate levels. Hrdlička (1921:160), in his study of dental morphology, notes that his research was "much interfered with by the exceedingly common partial to complete wear of the enamel and consequent obliteration of the finer modeling." Specifically, as noted, worn teeth lead to a loss of biological information, as well as a reduction in sample size. These issues are particularly problematic with skeletal and fossil series.

Many researchers have reported the need for caution when scoring traits on affected teeth (e.g., Nichol and Turner 1986; Wu and Turner 1993); however, less frequently considered is the possibility of misinterpreting morphological traits. For example, Morris (1970) cautions that worn lower molars with a deflecting wrinkle may resemble a Y-5 crown pattern. As a result, Y-5 frequencies can be inflated (Morris 1970). Still, these observations have not led to a much-needed focus on methodological issues regarding sample selection.

Methodologically, there are few strategies for dealing with worn teeth in studies of dental morphology. One "solution," employed by Hrdlička, was to fragment juvenile skeletal specimens to obtain unworn tooth crowns within the alveolar crypts. As he notes, only then was "…it possible in a number of important respects to arrive at some definite conclusions" (Hrdlička 1921:160). Fortunately, this destructive technique has yielded to an alternate method, that is, score only those teeth without excessive wear (e.g., Moorrees 1957) and accept necessary limitations of reduced sample size. Unfortunately, aside from anecdotal reports, there is no standard for how much is too much; nor are there any detailed studies of how wear affects individual traits and researchers.

We are aware of only one prior study that explicitly examined the effect of wear on frequencies of a morphological trait. The first author examined maxillary premolar accessory ridges (MxPARs) in human samples worldwide and created a scoring plaque for inclusion in the Arizona State University Dental Anthropology System (Burnett 1998; Burnett et al. 2010). MxPAR may be on the mesial and/or distal occlusal surface of the paracone and is therefore subject to occlusal wear, as noted previously (Scott 1973). The effect of increasing wear on MxPAR frequency was documented in a skeletal sample of 189 individuals from the site of Pecos Pueblo, New Mexico (Burnett 1998). Each tooth was scored employing Smith's (1984) eight-grade wear scale (Table 21.1) in addition to grades using the MxPAR plaque.

The analysis focused solely on grades 1–3 of Smith's scale; anything higher and the premolar cusps are reduced to a flattened surface lacking in detail. Not surprisingly, more teeth were deemed unscorable and excluded from analysis as wear increased. Nonetheless, MxPAR frequency at all four loci (mesial P1, distal P1, mesial P2, distal P2) decreased simultaneously as wear increased, with as much as a 59.7 percent difference in trait frequency between wear grades 1 and 3 at the distal P2 locus. This result should not have occurred if scoring was accurate, since MxPAR presence is controlled largely by genetics (Gilmore 1968; Wasser 1953); as such, it should be independent of behavioral components responsible for age-related wear. A minimum of two nonexclusive hypotheses may be in play (Burnett 1998): (1) trait downgrading from wear results in lower average grades and an increase

Table 21.1. *Wear grade descriptions across tooth types*

Grade	Incisor/Canine	Premolar	Molar
1	Unworn to polished or small facets (no dentin exposure)	Unworn to polished or small facets (no dentin exposure)	Unworn to polished or small facets (no dentin exposure)
2	Point or hairline of dentin exposure	Moderate cusp removal (blunting)	Moderate cusp removal (blunting). Human permanent molars show no more than 1 or 2 pinpoint exposures
3	Dentin line of distinct thickness	Full cusp removal and/or moderate dentin patches	Full cusp removal and/or pinpoint to moderate dentin exposure
4	Moderate dentin exposure no longer resembling a line	At least one large dentin exposure on one cusp	Several large dentin exposures, still discrete
5	Large dentin area with enamel rim complete	Two large dentin areas (may be slight coalescence)	Two dentinal areas coalesced
6	Large dentin area with enamel rim lost on one side or very thin enamel only	Dentinal areas coalesced, enamel rim still complete	Three dentinal areas coalesced, or four coalesced with enamel island
7	Enamel rim lost on two sides or small remnants of enamel remain	Full dentin exposure, loss of rim on at least one side	Dentin exposed on entire surface, enamel rim largely intact
8	Complete loss of crown, no enamel remaining; crown surface takes on shape of roots	Severe loss of crown height; crown surface takes on shape of roots	Severe loss of crown height, breakdown of enamel rim; crown surface takes on shape of roots

Note: Based on Smith (1984).

in the percentage of teeth not meeting the present/absent grade threshold, and (2) a previously unidentified sampling bias due to missing data exists. Analysis of the average degree of MxPAR expression suggested that its decline in frequency did not result from downgrading but was caused primarily by nonrandom missing data (Burnett 1998). This conclusion is apparent since the distribution of the trait's plaque grades does not migrate downward as wear increases (Figure 21.1). In other words, the peak of trait presence at wear grade 1 is MxPAR grade 2. If trait downgrading occurred from diminution of expression, then we would expect a shift toward higher frequencies of MxPAR grade 1 at higher levels of wear (2–3+). Instead, analysis of the average expression of those with grades 1 or above indicates little change in

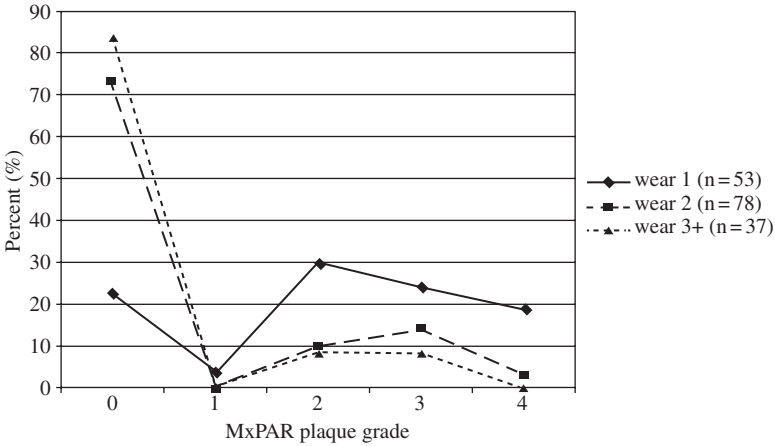

Figure 21.1. Distal P2 MxPAR grade distribution by degree of wear.

the plaque grade (Burnett 1998). It is apparent that some MxPARs may not be downgraded to 1 but are deemed absent (grade 0) instead – in effect skipping over the lowest grade expression. However, another factor appears to be nonrandom exclusion of worn teeth.

Missing data are common in many dental samples. Teeth in archaeological specimens may be missing ante- or post mortem, modified via cultural practices, and/or damaged by pathological (e.g., caries) or normal processes (e.g., attrition); otherwise, traits may simply be unobservable, for instance, due to calculus covering the crown or root traits obscured by alveolar bone. In these cases, researchers have largely ignored the nature of the missing data and focused on traits that could be recorded. However, implicit in this process is an untested assumption that the missing data did not differ in any way from those that were gathered.

The statistical treatment of missing data received much-needed attention in *Statistical Analysis with Missing Data* by Little and Rubin (2002), which differentiates among distinct categories. Data are said to be *missing completely at random* (MCAR) if the probability of missing data for a particular variable, Y, has no relationship to the value of Y and is also unrelated to other variables (Allison 2001). In dental morphology studies, testing the former statement would be difficult in the absence of longitudinal research, as there would be no reliable way to know the value of Y is absent. On the other hand, casts of the same individuals through time (e.g., Dahlberg's Pima Indian casts at Arizona State University) could provide insight into how missing data for variable Y are related to Y itself. However, the relationship between Y and another variable,

X, is more easily tested. If there are no differences in Y when analyzed by X, then the data can be considered as *observed at random* (Allison 2001). Yet, they still cannot be considered missing completely at random since we were unable to establish the absence of a relationship between missing data for a variable and the value of the variable itself. Data for Y can only be considered *missing at random* if "the probability of missing data on Y is unrelated to the value of Y, after controlling for other variables in the analysis" (Allison 2001:4).

In the case of MxPAR, data could not be said to be missing completely at random since there is no way to test whether they were observed at random. Despite increasing percentages of teeth being excluded from analysis, those actually scored as wear increased were less likely to be listed as having MxPAR than excluded teeth. Importantly, this issue occurred even at low to moderate wear levels (Burnett 1998).

21.4 Materials and methods

For the present study, up to four morphological traits were recorded by two observers in an archaeological sample of 129 Nubians from the site of Semna South (Zabkar and Zabkar 1982). The Arizona State University Dental Anthropology System (ASUDAS) (Turner et al. 1991) was used for data collection. Observer 1 had 4 years of experience with the ASUDAS, while observer 2 was new to the system. Neither observer was aware of the results of the other, or the purpose of the project.

The four traits are UI1 shoveling, UC distal accessory ridge, LM2 cusp number, and UM2 hypocone. They encompass a range of features throughout the dental arch that consist of minimal to substantial buttressing of the occlusal and lingual surface (shoveling), relatively minor ridge formation on the occlusal surface (distal accessory ridge), and variation in both molar cusp number and size (hypocone).

Shoveling data on the upper central incisors were collected using the ASUDAS UI1 shoveling plaque seen in Figure 21.2a; it has seven grades of expression (0–6) (Turner et al. 1991). A breakpoint of grade 2 was used for analysis (i.e., 2–6 are considered present). The distal accessory ridge of the upper canine was scored with the aid of the plaque in Figure 21.2b; it depicts six grades ranging from absence (grade 0) to a very pronounced ridge (grade 5) (Turner et al. 1991). A grade 2 breakpoint was used for this trait as well. Lower second molars were scored as having four (i.e., protoconid, metaconid, hypoconid, entoconid), five (addition of hypoconulid), or six cusps (five plus entoconulid) (Turner et al. 1991). Trait presence was based on occurrence of the hypoconulid (cusp 5); there is no ASUDAS plaque. The final trait was

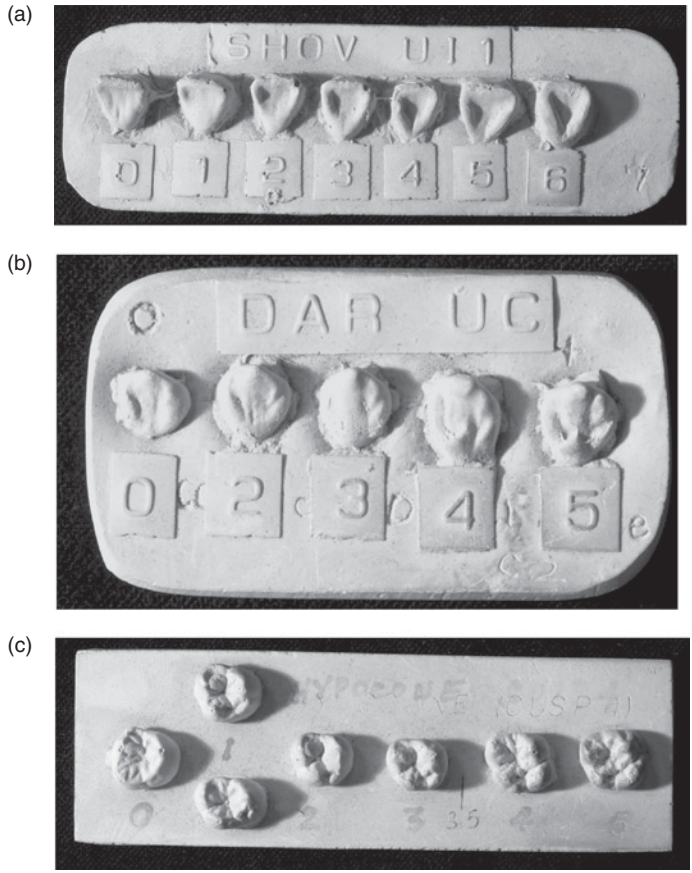

Figure 21.2. ASU Dental Anthropology System scoring plaques: (a) UI1 shoveling, (b) UC distal accessory ridge, (c) hypocone.

scored using the ASUDAS hypocone plaque (Figure 21.2c) and comprises seven grades; the breakpoint was again set at 2.

The degree of wear for each tooth in the Nubian sample was assessed after trait recording using Smith's (1984) scoring system. This system consists of descriptions (Table 21.1) and images depicting grade 1 – no wear or small facets with no dentine exposure – through grade 8 – effectively a root stump with little or no crown remaining. Moderate dentine exposure does not occur until grade 4.

Wear data by trait were initially partitioned into at least three categories for illustrative purposes (refer to following figures), prior to subsuming them into low and high wear categories for statistical analyses (later). Similarly, ASUDAS

scores were converted to present/absent dichotomies to facilitate comparisons. In this case, the individual count method was used for trait frequency calculation; the highest plaque grade was used to represent individual trait expression in cases where antimere grade asymmetry exists. This approach assumes that the expression best reflects the genetic potential for each trait (Scott 2008). Lastly, Fisher's exact tests were used to identify significant differences (α = 0.05) in trait frequencies between the low and high wear groups. Thus, the resulting 2 × 2 contingency tables (not shown) consist of trait dichotomies in the rows and wear dichotomies in the columns.

21.5 Results

Sample sizes for UI1 shoveling and UC distal accessory ridge scored by observer 2 were too small for meaningful comparison when subdivided by wear level. Accordingly, our analysis here focuses on data collected by observer 1 on all four morphological traits, and those collected by observer 2 for both molar traits.

21.5.1 UI1 shoveling

Shoveling on upper central incisors scored by observer 1 demonstrates a wear-related trend, with trait frequency declining as wear increased (Table 21.2). A graph (Figure 21.3) of shoveling grades by wear level (1, 2, and 3–4) indicates that some teeth at wear grade 1 were assigned a trait grade of 0 – with the percentage increasing at successively higher wear. Conversely, the frequency of grade 3 shoveling, that is, the most pronounced in this sample, was highest at wear grade 1 and decreased with progressive wear. The peak of the distribution appears to migrate toward the left, that is, lower shoveling grades with increasing wear; the implication is that increasing wear causes a reduction in the degree of expression scored. The difference in trait frequency between the low (1) and high (3–4) wear categories is significant ($p = 0.036$).

21.5.2 UC distal accessory ridge

The findings for UC distal accessory ridge were similar, where increasing tooth wear corresponds to a decrease in trait frequency (Table 21.2). This result is

Table 21.2. *Trait frequencies by wear grade*

	Wear grades[a]			
Trait – Observer	1	2	3+4	Total sample
UI SHOV – Obs1	66.7% (n = 9)	33.3% (n = 18)	20.0% (n = 15)	35.7% (n = 42)
UC DAR – Obs1	50.0% (n = 10)	28.0% (n = 25)	14.3% (n = 14)	28.6% (n = 49)
UM2 Hypocone – Obs1	80.8% (n = 26)	83.3% (n = 42)	73.5% (n = 34)	79.4% (n = 102)
UM2 Hypocone – Obs2	88.5% (n = 26)	94.7% (n = 38)	100.0% (n = 20)	94.1% (n = 84)

	Wear grades[a]				
	1	2	3	4+5	Total sample
LM2 Cusp# – Obs1	45.0% (n = 20)	24.1% (n = 29)	21.2% (n = 33)	13.3% (n = 15)	25.8% (n = 97)
LM2 Cusp# – Obs2	44.4% (n = 18)	24.1% (n = 29)	25.8% (n = 31	15.4% (n = 13)	27.5% (n = 91)

Note:
[a] According to classification developed by Smith (1984). See Table 21.1.

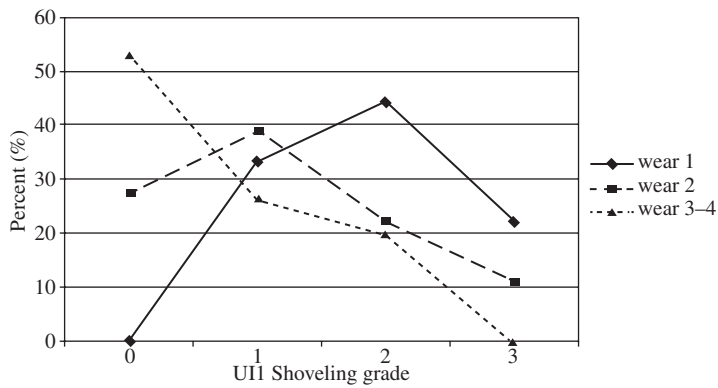

Figure 21.3. UI1 shoveling (Obs. 1) grade distribution by degree of wear.

likely related to scoring the trait at a lower grade in worn teeth, and vice versa (Figure 21.4), though the pattern is less obvious than with shoveling. The difference in trait frequency between the low and high wear grades is not significant ($p = 0.085$).

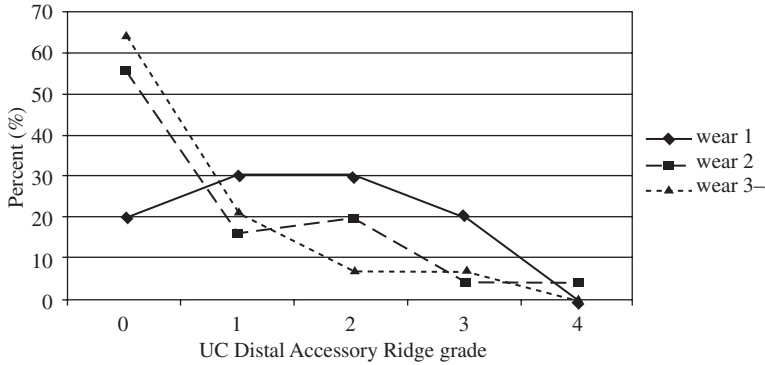

Figure 21.4. UC DAR (Obs. 1) grade distribution by degree of wear.

21.5.3 LM2 cusp number

A decline in the frequency of five-cusped teeth is seen at the various wear stages for both observers 1 and 2 (Table 21.2). Teeth with grade 1 wear exhibit the highest frequency of five+ cusps (44.4–45.0 percent); moderately lower frequencies are evident at wear grades 2 (both observers with 24.1 percent) and 3 (21.2–25.8 percent) and are dramatically lower at grade 4 or 5 (13.3–15.4 percent). Analysis by degree of expression is not necessary because all teeth were recorded as having either four or five cusps. As a result, it is difficult to determine whether frequency change resulted from trait downgrading or issues with the MCAR assumption. For observer 1, LM2 cusp number frequency at wear grade 1 is significantly different from that at wear grades of 3+ ($p = 0.033$), but not when compared solely to the smaller sample comprising wear grades 4 and 5. Although the wear-related trend is the same, LM2 cusp number frequencies at wear grade 1 from observer 2 are not statistically different from those recorded at grades 4 and 5 ($p = 0.124$); sample size may be an issue.

21.5.4 UM2 hypocone

No wear-related trends are evident in hypocone frequencies recorded by observer 1 (Table 21.2). Trait frequency increases from wear grade 1 to 2 but declines at grades 3–4. Relative to the other traits, the frequency range is narrow (73.5–83.3 percent) across wear categories. As a result, differences between low and high wear grades are not significant ($p = 0.555$). The distribution of hypocone scores by observer 2 (Figure 21.5) demonstrates the

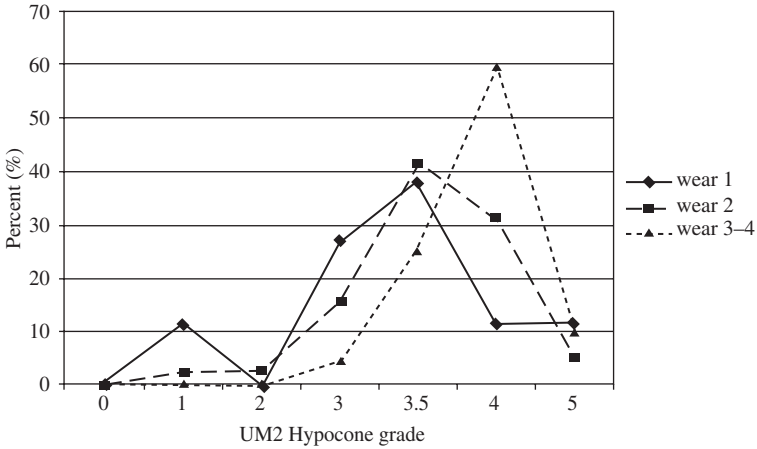

Figure 21.5. UM2 hypocone (Obs. 2) grade distribution by degree of wear.

effects of (1) wear, that is, slight change in trait appearance results in its being recorded at a slightly lower or higher grade; and (2) bias from violating the MCAR assumption. Trait grade drift is apparent since higher grade scores occur more frequently as wear increases. Alternatively, trait grade 1, a small wrinkle where the hypocone would develop is not scored at all as wear increases, resulting in missing data since there is no concomitant increase in those scored as grade 0. This finding is suggestive of MCAR violations, where the missing data are not missing randomly. Observer 2 trait frequencies then consistently increase as wear increases (Table 21.2). A hypocone score of 2 or higher was recorded on 88.5 percent of teeth at wear grade 1, along with 94.7 percent at wear grade 2 and 100 percent at wear grades 3–4. Still, the frequency differences between wear grades 1 and 3–4 are not statistically significant ($p = 0.246$); that, again, may relate to the narrow frequency range in these small samples.

21.6 Discussion

Results of our experiment suggest dental wear can lead to frequency issues in the analysis of morphological traits. Affected traits may be of different types and occur in any tooth class. As seen here, and previously by Burnett (1998), the principal effect is regressive: trait frequencies decline with increasing wear as a result of trait downgrading or MCAR violations. Three of the present

four traits (UI shoveling, UC DAR, LM2 cusp number), along with MxPAR (Burnett 1998), display this pattern; the UM2 hypocone is characterized by a frequency increase, at least for one observer. Moreover, there can be significant frequency differences between subsamples with low versus high wear.

The strength of the effect that wear has on trait scoring may differ on the basis of tooth number (e.g., M1, M2, or M3), or trait loci on the tooth (e.g., mesial vs. distal UP1 or UP2 accessory marginal tubercles). One reason may be the offset of teeth between arches thought to permit stability in intercuspal position, as well as to minimize interference between opposing cusps in mastication (Kraus et al. 1969). With the exception of LI1 and UM3, most teeth occlude with two others in the opposing arcade. Since mandibular teeth are shifted mesially and lingually relative to their isomeres, a maxillary tooth will contact both its opposing counterpart and the member behind it. For example, UP2 occludes with LP2 and LM1. Of course, the area of UP2 that occludes with each of these teeth may not be equal; the result is differential wear on the buccal cusp. Across-crown disparities may cause wear bias to be more pronounced on one side of the tooth (e.g., MxPAR).

Newly conducted Pearson's correlations of wear and MxPAR grades from prior data (Burnett 1998) indicate stronger negative correlations (i.e., as wear increases, trait grade decreases) on the distal loci (DLP1 $r = -0.408$, $p < 0.001$; DRP1 $r = -0.300$, $p < 0.001$; DLP2 $r = -0.484$, $p < 0.001$; DRP2 $r = -0.427$, $p < 0.001$) relative to the mesial loci (MLP1 $r = -0.289$, $p < 0.001$; MRP1 $r = -0.140$, $p < 0.050$; MLP2 $r = -0.168$, $p = 0.056$; MRP2 $r = -0.279$, $p < 0.050$). The stronger relationship between wear and trait grades at distal loci is true regardless of antimere and premolar position (first or second); this pattern is likely due to the location and direction of opposing cusps during mastication, to yield greater wear distally on the paracone (Kraus et al. 1969).

The wear-related factors described here imply that analyses of dental morphology in archaeological or paleontological material, where heavy tooth wear is common, may be problematic. Kaifu (2000) specifically addressed this issue by recording tooth wear in adult specimens attributed to the genus *Homo* over the past two million years, with recent humans represented by a sample of Jomon. Wear was assessed using the same scale employed here (Smith 1984). Median wear for dentally mature *Homo* individuals exceeded grade 4 for upper and lower incisors, canines, and first molars; few exhibited grade of 2 or less. Predictably, later erupting upper and lower second molars fared slightly better with median wear scores of 3 to 4.5.

Moreover, our results may explain some age-related patterns reported in prior studies of archaeological samples. For example, Powell (1995:155) suggests that the ability to observe a trait may depend on age progressive

factors like attrition, as well as caries and calculus; yet he states that this environmental variation "should have been eliminated by deleting observations where wear or calculus buildups obscured morphological features of the tooth, but it is possible that some residual age effects remained." His analysis reported that the following traits had a significant age effect: UM1 metacone, UM2 metaconule, LM1 and LM3 metaconulid size, UM2 and LP2 enamel extensions, LM2 and LM3 groove patterns, LM1 cusp number, LM3 distal trigonid crest, and LM3 congenital absence. All traits, except LP2 enamel extension, were characterized by frequency regression, leading to the conclusion that on some occasions "a trait was more likely to be scored as a low grade (later converted to 'absent') in older individuals due to some unrecognized effect of dental attrition" (Powell 1995:155). While trait downgrading is possible as seen here, nonrandom missing data are another issue facing dental anthropologists.

Turner (2002) suggests that wear can modify a Sinodont dentition to resemble that of a Sundadont if individual traits are scored at lower grades. This possibility could account for some early- to mid-Holocene New World dentitions variably identified as Sundadont (Chatters 2000) or, minimally, non-Sinodont (Powell et al. 1999; Powell 2005). Although Powell (1995) removed traits showing significant age-related frequency differences, additional minor biases may have persisted since statistical significance is difficult to establish in small samples. As an example, consider the observer 2 results for LM2 cusp number; the frequency difference between the high and low wear grades was ~30 percent, though not statistically significant because of sample size at higher wear.

Of course, dental wear may not be the only factor in trait frequency bias. Berry (1976) observed that attrition was an issue with foragers, but that caries was the most problematic factor in recording dental morphology among agriculturalist groups. Thus, the MCAR assumption could be violated because of the pathogenic predisposition of some traits. As Berry (1976) went on to say, "it is possible that certain of the variants here described render the tooth more or less caries prone so that the sample incidence could alter with time as caries affect variant bearing teeth differentially." Buccal pits on mandibular molars are a prime example (Hartney 1981). With increasing age and exposure to cariogenic foods, caries are more likely to be present. In a large ossuary sample, Pfeiffer (1979) identified a significantly lower frequency of buccal pits in individuals more than 18 years of age. The causal mechanism is likely caries with antemortem loss. Tooth loss is another violation of the MCAR assumption because remaining teeth in the sample are less likely to have buccal pits. Pits and grooves on the lingual, buccal, and occlusal surfaces

in other teeth are also known to be sites of caries susceptibility (Awazawa et al. 1989; Juhl 1983).

21.7 Now what?

We want to stress vigorously that the findings reported here do not portend the demise of dental morphological studies. Two key multifactorial caveats exist that endorse continuation of the latter, albeit with some extra measure of attention paid to the compilation and comparison of certain samples.

First, the previous (Burnett 1998) and present findings represent preliminary attempts to quantify the effects of dental wear on morphological scoring. Three associated deficiencies to be addressed in the future are summarized: (1) All observers at the time of recording were relatively inexperienced – with the most knowledgeable individual (observer 1) having just 4 years of familiarity with the ASUDAS; more advanced researchers, with likely better insight into how wear may "erase" or "enhance" crown features, need to be involved. (2) Only five traits, four of which were assessed here, were tested for potential wear-related bias. Of the latter, just two were recorded by more than one individual to evaluate interobserver variation. In some cases, statistically significant differences were observed in trait by wear grades; yet not all differences were significant – largely because of small sample sizes. Ideally, all ASUDAS traits will eventually be tested, by multiple observers, for wear bias. (3) The archaeological dentitions used for the prior (Burnett 1998) and present studies are not ideal for trait-by-wear comparisons. One issue, as noted, is sample size – especially at higher wear levels that preclude fine-grained statistical comparisons. Another important concern is the lack of actual trait data in worn crowns, that is, the described trends are based on "presumed" trait presence and expression. As mentioned previously, the ideal sample would be longitudinal in nature, where dental casts are taken throughout the lives of many individuals (e.g., the ASU Dahlberg's Pima Indian casts); such a study would empirically gauge the effect of wear on trait expression.

Second, of greatest importance is the success of prior dental morphological studies that, because of their sheer number, preclude a full list of citations in this short chapter. In brief, several Plio-Pleistocene (Irish 1998; Irish and Guatelli-Steinberg 2003; Martinón-Torres et al. 2007; Stringer et al. 1997) and innumerable post-Pleistocene samples have been recorded, described, and compared using the ASUDAS; the more recent samples include analyses at local, regional, continental, and global scales, including those from Africa (Irish 1997, 1998, 2000, 2005, 2006), Asia (Turner 1985, 1992; Haeussler

1996; Hanihara 1992), Australia (Turner 1992), Europe (Turner 1984, 1985; Adler 2005), India (Hawkey 1998, 2004; Lukacs et al. 1998), the Middle East (Roler 1992; Lipschultz 1996), the New World (Scott et al. 1983; Turner 1985, 1992; Haeussler 1996), and Oceania (Scott and Turner 1997), among others. Without repeating that which has been duly reported in detail elsewhere (e.g., Scott and Turner 1997), the findings and relationships described in these publications mirror or better those based on other skeletal morphometric methods, genetics, and linguistics and are highly concordant with documented population history; dental morphological study with the ASUDAS does work despite varying levels of crown wear in these many hundreds of samples and tens of thousands of individuals.

With these caveats acknowledged, we have a few recommendations for researchers. If our results are predictive of how other traits could be affected, there is potential for significant frequency differences among subsamples exhibiting low versus high wear; as such, care should be taken when comparing samples possessing notably different wear patterns and profiles. The implications are most critical where heavy wear is the norm, such as in archaeological and fossil specimens. Such samples are often small to begin with, particularly in the case of fossil hominins (Teaford et al. 2002). Restricting sample size more by rejecting worn teeth will further reduce statistical power. Nonetheless, the alternative may be to use data that obfuscate the underlying pattern(s) of biological variation. So what can be done considering the limitations of samples in the real world of anthropology?

Until such time as all ASUDAS traits may be studied according to wear level, we suggest that the latter could be graded using a fine-grained scheme like Smith's (1984), beyond the more basic approach currently part of the ASUDAS (Turner et al. 1991). Ideally, analyses could then be conducted to examine the potential of wear bias for specific traits and observers to assist in composition of adequate, unbiased samples. Simply put, samples with widely divergent wear would not be compared. If this ideal scenario is impossible, as is likely with fossil and archaeological material, obvious differential wear among samples should be documented, and, at a minimum, possible implications can be discussed and caution exercised in the interpretation of results. Otherwise, use of crown features that are least affected (e.g., UI1 winging, tuberculum dentale, peg-reduced teeth, LM2 torsomolar angle), or noncrown ASUDAS traits, including intraoral osseous variants and root features that are not affected by wear, could be preferentially used. In sum, although some caution is warranted, we believe that further methodological refinement will foster more productive analyses of human dental morphology.

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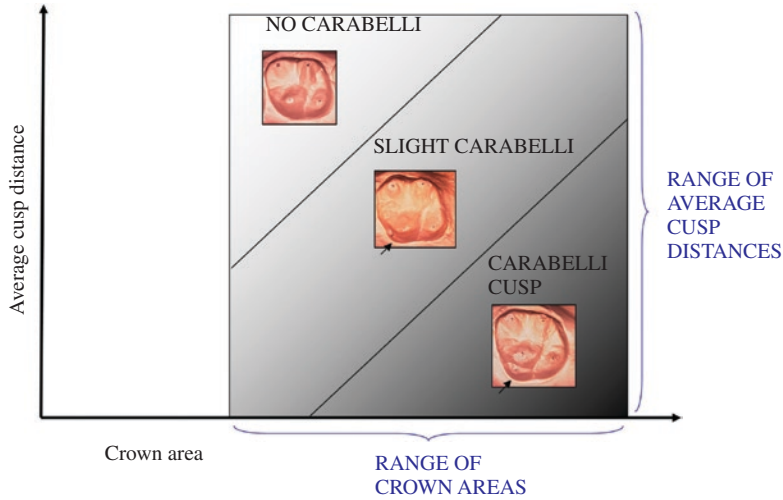

Figure 4.1. Predicted associations between cusp spacing and tooth size with Carabelli trait expression.

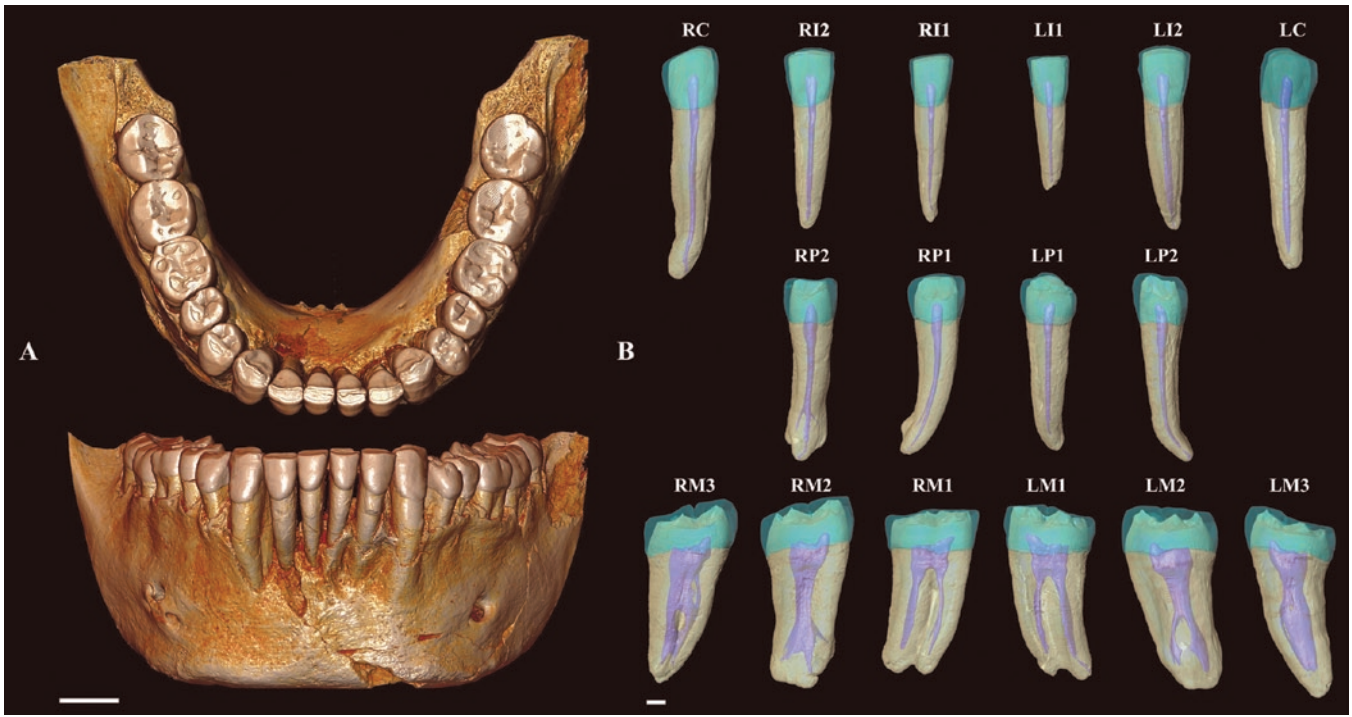

Figure 11.1. The lower dentition of the adult Neanderthal Regourdou 1. Image A shows the microtomographic-based 3D reconstruction of the mandible in occlusal (top) and frontal (bottom) views (scale bar, 1 cm). Image B shows the entire series of virtually extracted teeth (in labial/buccal view) rendered in transparency (scale bar, 2.5 mm).

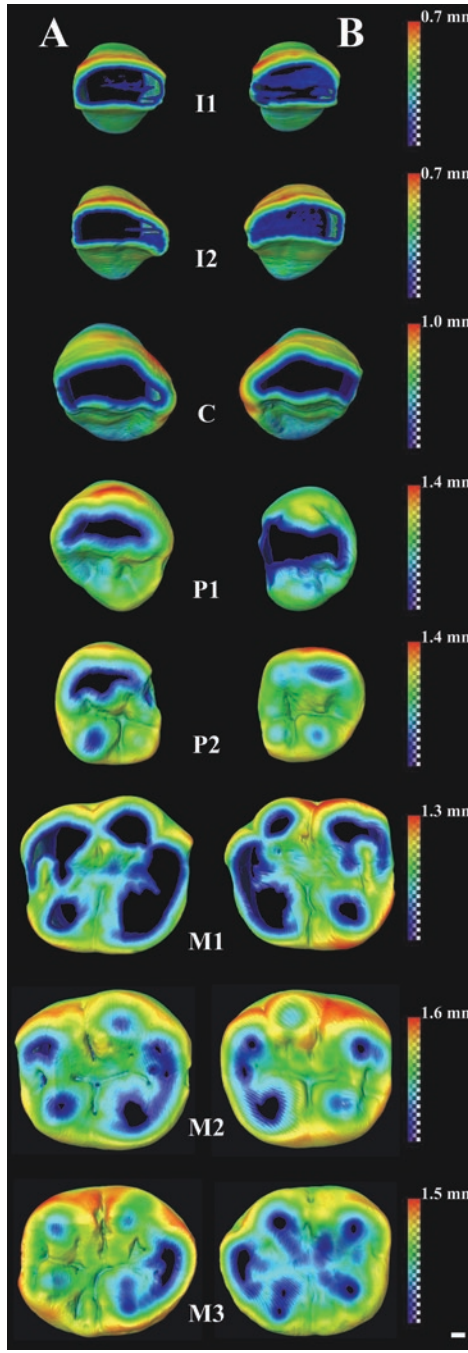

Figure 11.2. Regourdou 1. Comparative enamel thickness cartographies of the virtually reconstructed right (A) and left (B) lower tooth crowns in occlusal view. Topographic variation is rendered by a tooth-specific thickness-related scale (original version in pseudocolors) ranging from dark gray (relatively thin to entirely removed enamel) through light gray (relatively thicker enamel). Scale bar, 1 mm.

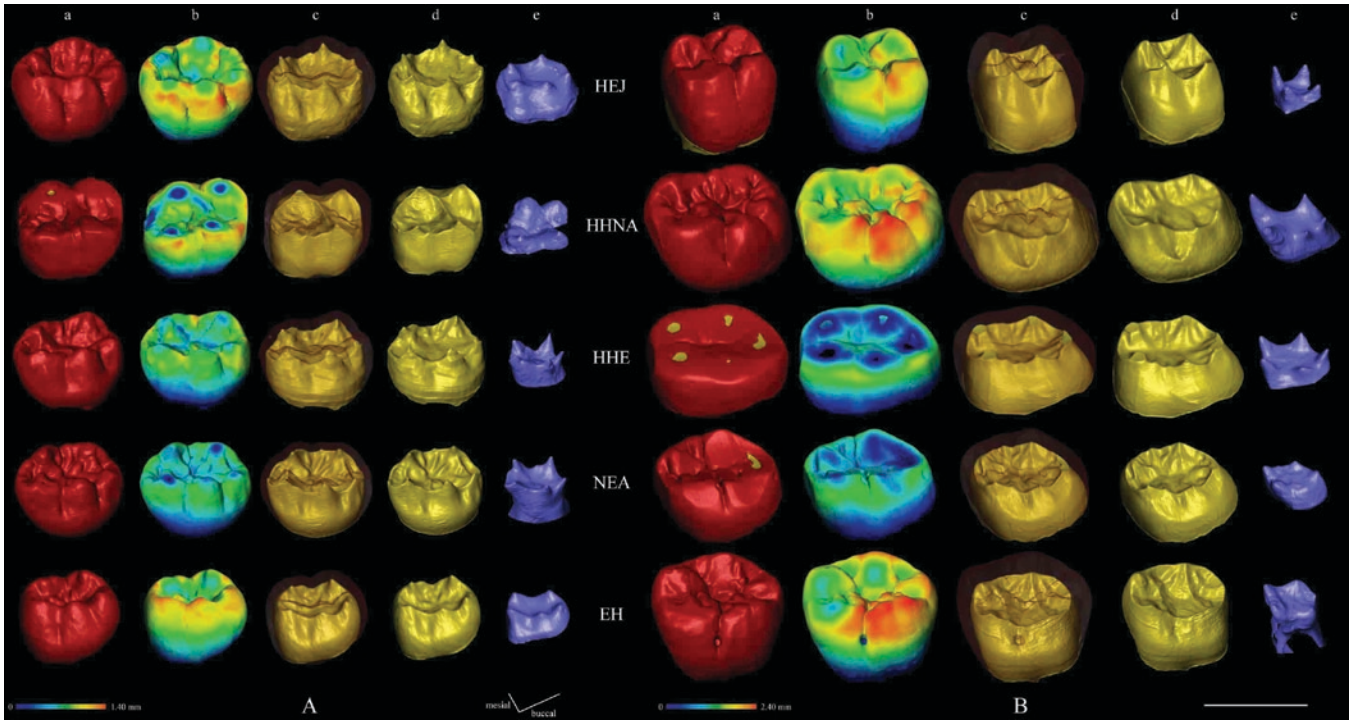

Figure 11.3. Microtomographic-based virtual rendering in occlusal-buccal view of the outer crown (a); the enamel thickness variation (b); the enamel-dentine junction (EDJ) with the enamel in semi-transparency (c); the EDJ (d); and the pulp cavity (e) (original version in pseudocolors) comparatively provided in deciduous (A) and permanent (B) molar crowns representing five fossil and extant human taxa/populations. In (b), topographic variation is rendered by a thickness-related scale ranging from dark gray (relatively thin to entirely removed enamel) through light gray (relatively thicker enamel). EH: extant humans; HEJ: *H. erectus* from Java; HHE: European late *H. heidelbergensis*; HHNA: early *H. heidelbergensis* from North Africa; NEA: European Neanderthals. See the text for details on the composition of the samples. Scale bar, 1 cm.

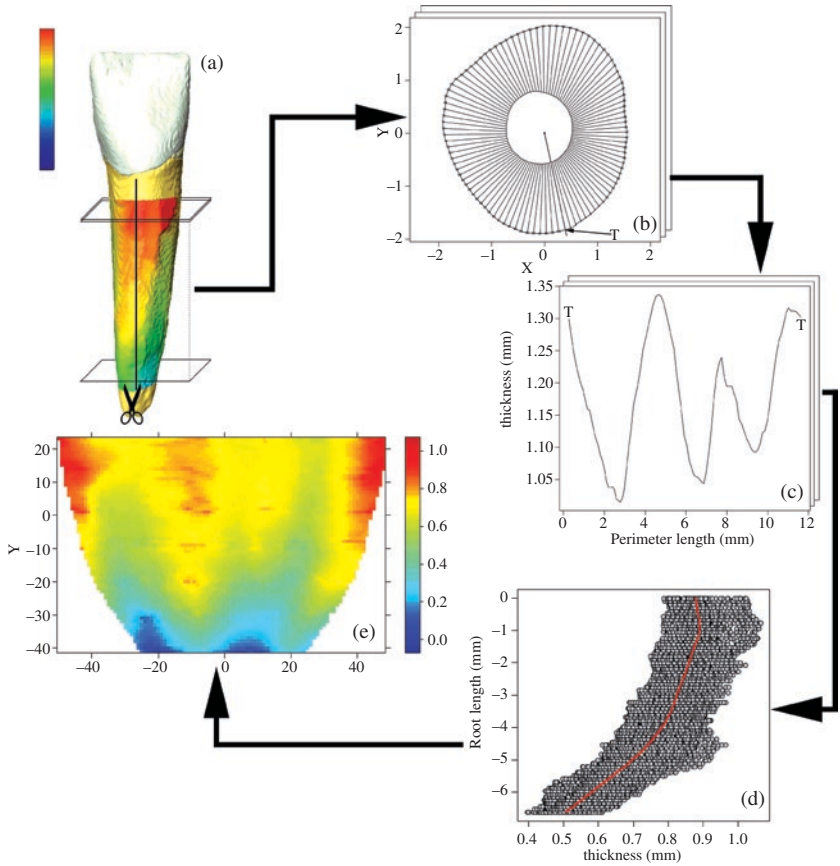

Figure 11.4. Schematic representation of the process of morphometric map (MM) generation specifically adapted to irregularly shaped 3D structures such as tooth roots. (a) microtomographic-based rendering of a human deciduous incisor (buccal view) showing dentine thickness variation. The vertical line represents the cutting edge for root unrolling. (b) virtual cross section of the root at a generic level Z_i, where X and Y are the original coordinates of the translated surface with the origin set at the centroid, and T indicates the cutting point. (c) profile of dentine thickness variation at Z_i level. (d) dentine thickness variation expressed through the $Z_1 \ldots Z_n$ entire set of virtual cross sections (the line indicates the mean values). (e) the MM of the virtually unrolled root showing dentine thickness topographic variation. In A and E, variation is rendered by a thickness-related scale (original version in pseudocolors). In E, the darker areas appearing near the bottom and those obliquely/vertically oriented in the middle-superior part of the map, respectively, correspond to the thinnest and the thickest regions, the remaining light gray areas indicating intermediate values.

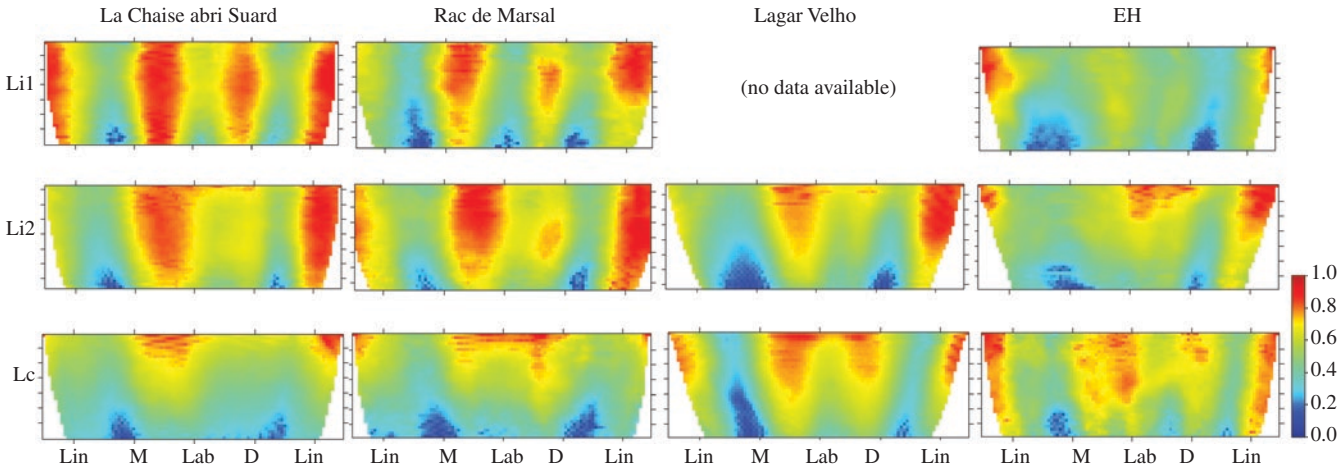

Figure 11.5. Comparative standardized morphometric maps (MMs) of virtually unrolled tooth roots (portion 50–85 percent of the total root length, where 85 percent [upper] is toward the tooth cervix) of lower deciduous incisors (Li1 and Li2) and canines (Lc) from two Neanderthal specimens (La Chaise abri Suard and Roc de Marsal), the Upper Paleolithic (Gravettian) child from Lagar Velho, and extant humans (EH, consensus maps). Dentine topographic variation is rendered by a thickness-related scale (original version in pseudocolors). In all cases, the darker areas appearing near the bottom and those obliquely/vertically oriented in the middle-superior part of the maps, respectively, correspond to the thinnest and the thickest regions, the remaining light gray areas indicating intermediate values. Lin: lingual; M: mesial; Lab: labial; D: distal.

Figure 13.3. Characteristic “Eurodont” traits: (A) Carabelli’s cusp on UM1 so large that is shows exposed dentine, (B) typical spatulate and mostly featureless upper incisors, (C) two-rooted lower canine, (E) five-cusped LM1 and four-cusped LM2.

Figure 17.1. Key morphological features of the Native American dentition. A. Extreme shoveling and double shoveling (white arrows) in a maxillary incisor. B. Mandibular premolar odontome. C. Lower left first molar with cusp 6 and deflecting wrinkle.